Successional changes of soil animals in relation to fungal colonization and nutrient dynamics of decomposing pine needles

1998

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Acknowledgements

This study was carried out at the laboratory of Forest Ecology, Faculty of Agriculture, Kyoto University, under the supervising of Dr. H. Takeda, to whom I wish to express my sincere gratitude for his helpful guidance and valuable advice in all of field work and laboratory analysis and writing the thesis.

I am indebted to Prof. A. Takafuji and Prof. H. Watanebe of Kyoto University for their critical reading of the manuscript and helpful comments.

I would like to thank to Dr. M. Luxton for his kindness in reading and correcting the manuscript, to Dr. J. Aoki and Dr. M. Ito for their guidance and identifying Cryptostigmata, to Dr. R. Yosii for his guidance and identifying Collembola.

I also thank Dr. Iwatsubo, Dr. Kawaguchi, Dr. Tokuchi and members of the Forest Ecological Laboratory for their helpful discussion.

Dr. Enoki, Mr.Yamashita, Mr. Ogino and Miss Namikawa helped me in the chemical analysis of decomposing litter. I also thank for the assistance of Mr. Kasuya and Mr. Kato in the field work.

Finally, I want to thank my parents, my brother and my sister for their understanding and heartful support.

Motohiro Hasegawa

Contents

1. Introduction

Decomposition processes and soil fauna

In forest ecosystems, over ninety percent of net primary production flows into the soils as dead organic matter (Vogt et al. 1986), and provides the food and habitat for the heterotrophic decomposers such as microorganisms and animals. The dead organic matter is metabolized by decomposers, and nutrients in the organic matter are mineralized. The nutrients are reabsorbed by plants through their fine roots, and are utilized for the biosynthesis. The rates of primary production are depending upon the rates of nutrient supply through the decomposition process in soils. Thus, the activities of decomposers are important for the nutrient cycling and maintenance of ecosystem productivity (Swift et al. 1979, Waring and Schlesinger 1985). Soil animals have the direct and indirect roles in the decomposition processes. Soil animals directly contribute to the decomposition by metabolizing organic matter to the CO_2. The indirect roles include the interaction between soil animals and microorganisms. The soil animals influence the decomposition processes through the grazing of microorganisms, and modifying the physicochemical conditions for the microorganisms.

The decomposition of litter proceeds with microbial activities (Berg & Söderström 1979). On the basis of the energy (carbon) flows in forest ecosystems, soil microbial populations account for about 95 to 99% of the total heterotrophic respiration. Soil animals show a minor contribution for the carbon cycling in the soil systems. The heterotrophic respiration of soil animals ranges from 1 - 5% of total heterotrophic respiration in coniferous forest soils with mor or moder humus forms (Huhta and Koskenniemi 1975, Persson et al. 1980), to about 10% in nutrient rich forest with mull humus forms or mesic grasslands (Reichle 1977, Schaefer 1990, Coulson and Whittaker 1978, Persson 1989). The high contributions of soil animals have been often reported in the soils with mull humus forms, where litter feeding macrofauna such as earthworms are dominant (Petersen & Luxton 1982, Schaefer and Schauermann 1990). In both nutrient poor and rich forest soils, the direct roles of soil animals are rather small compared with the roles of microbial populations. Thus, soil animals contribute to the decomposition processes through their indirect roles.

Decomposition processes in the soil systems occur as a result of interactions between microbial and soil animal populations (Swift et al. 1979). So the roles of soil animals are not simply evaluated by the direct role, such as their own contribution to the

ecosystem metabolism. Since the late 1970s, soil zoologists have been much focused on the indirect effects of soil animals to the decomposition processes. Visser (1985) showed the three different mechanisms for the interaction between soil animals and microorganisms in the decomposition processes; i.e. 1) comminution and channeling, 2) grazing and 3) dispersal.

Comminution and channeling have been shown mainly in macrofauna such as Myriapoda and Isopoda (Anderson & Bignell 1980, Hanlon & Anderson 1980). Soil animals modify the physicochemical condition of litter substrates and influence the microbial population. The structure of soil is changed through their feeding and foraging activities and faeces production of soil animals. The environment of a habitat for the microorganisms could be influenced by the structure of soil. The mechanisms of grazing can be occurred through the feeding of microorganisms by the soil animals. The grazing effects have been shown for the microarthropods such as Collembola and Cryptostigmata (Hanlon & Anderson 1979). The grazing influences the decomposition processes through the change of microorganism populations. The grazing promotes the growth of new colonies after removing senescent hyphae (Hanlon 1981). Soil microarthropods prefer to graze fungus rather than bacteria populations. This feeding preference influences the composition of microbial populations (Hanlon & Anderson 1979). The grazing changes the result of the competition between microorganism species (Newell 1984 a, b). The dispersal effect of soil animals is occurred by carrying the propagules of microorganisms. The propagules might be attached to the bodies of soil animals or kept in the gut of animals (Visser 1987). The survival rate of the propagules depends on the situation of the studies (Lussenhop 1992).

Indirect effects of soil animals in the decomposition processes have been demonstrated in the laboratory conditions. Further these laboratory studies followed only few weeks or months. In natural conditions, decomposition processes take over a year to several years. So the short term laboratory experiments are oversimplified the interactions between soil animals and microbial populations during the decomposition processes. Further, the interaction between soil animals and microbial populations may be changed with the decomposition stages of litter. The indirect roles of soil animals have not been related with the decomposition stages of litter. Thus, the study of the indirect role of soil animals should be related with the decomposition stages with different nutrient and microbial conditions during long term decomposition processes in the natural conditions.

Successional studies of soil animals during decomposition processes

Soil animal population and community have been studied for the understanding of the decomposition processes in forest ecosystems. Soil animal communities provide excellent systems for testing hypotheses in current community ecology. The soil system is discrete and the soil animal communities are also rather discrete compared with other terrestrial communities. Among the soil animals, soil microarthropods, including Collembola and Acari are very abundant and the communities are species rich in the soil habitat. Sampling and experimental manipulations of soil arthropods are relatively easier than with other animals, and the organization of soil animals may be related to the decomposition processes.

The community organization of soil animals has been a central topic in the soil ecology. During the International Biological Program, abundances of various groups of soil animals have studied in various ecosystems all over the world (Petersen and Luxton 1982). These studies suggested that in the nutrient poor soils with mor or moder humus forms, Collembola and Cryptostigmata are numerically abundant groups among the soil animals during decomposition of plant litter (Swift et al. 1979, Coleman and Crossley 1995). The abundances of Collembola in coniferous forest soils were 25 X 10^3 m^{-2} in spruce forest (Huhta et al. 1967), 60 X 10^3 m^{-2} in a Scots pine forest (Person et al 1980), 145-244 X 10^3 m^{-2} in Norwegian source forest (Petersen and Luxton 1982). The abundances of Cryptostigmata in coniferous forest soils were 5-20 X 10^3 m^{-2} in Tsuga and Abies Forest (Kitazawa 1977), 212 X 10^3 m^{-2} in spruce forest (Huhta and Koskenniemi 1975), 425 X 10^3 m^{-2} in a Scots pine forest (Person et al. 1980).

Ecological studies have been done to explain the distribution and abundances of soil microarthropods in soils. Distribution patterns of soil microarthropods have been related to the habitat conditions such as chemical and physical properties of soils and development of soil organic layers and vegetation types (Hågvar 1984; Hågvar & Abrahamsen 1984; Reddy & Venkataiah 1989; Teuben & Smidt 1992). Studies of distribution patterns of these microarthropod communities have been showing the niche classifications in the communities with the depths in the organic matter layers (Anderson 1971, Usher 1970, 1975; Faber & Joosse 1993; Kampichler 1990; Luxton 1981; Pande & Berthet 1975; Takeda 1978; Wood 1967).

These descriptive studies on the distribution and abundances of soil animal populations and communities give a clue for the experimental manipulation studies of soil animals. The manipulation study for the effects of litter supply (Huhta 1976; Ponge et al.

1993) suggested that the community of soil animals depends on the resource from the vegetation production. The litter condition during the decomposition processes might be the main factor determining the structure of soil animal communities. Takeda (1987) concluded that Collembola community was dynamically maintained in an equilibrium state by the response of individual populations to the renewal and decomposition processes of litter in the soil habitat.

Among the field experimental methods of soil animals, litter bag methods (Crossley & Hoglund 1962) have been often used to study the faunal changes (succession) during decomposition processes (Metz and Farrier 1969, Anderson 1975; Hågvar & Kjøndal 1981; Takeda 1988). In the litter bag method, decomposing litter can be monitored together with the faunal colonization process. But few litter bag studies (Takeda 1995) have related soil animal colonization surveys to the litter condition during the decomposition processes. Thus, joint studies of dynamics of decomposing litter and soil animal populations are needed for the interpretation of successional patterns of soil animals. These studies give a clue for the understanding of the organization and function of soil animals in soil systems.

The decomposition of needle litter as the interactive process of microorganisms and soil animals

The role of decomposers is especially important for the nutrient poor coniferous forests, where the availability of nutrients to plants is low (Vitousek 1982). In nutrient poor sites, soil humus form shows a mor or moder type with a thick organic layer and plants depend on the limited nutrients mineralized from the organic layer (Müller 1887, Handley 1954, Green et al. 1993). So, decomposition of coniferous needles has been intensively studied in forest ecosystems in North Europe (Berg 1986) and North America (Aber et al. 1990). In these studies, the decomposition processes of needles have been correlated with variable substrate qualities (Heal et al. 1997) ; eg. nitrogen concentration (McClaugherty et al. 1985), nitrogen and lignin content (Edmonds 1984; Berg 1986; Stohlgren 1988), lignin / N ratio (Tietema 1993), C/N ratio and lignocellulose (Mellilo et al. 1989). Berg et al. (1993) concluded that at any one site most of the variation in mass-loss rates could be explained by the litter-quality variables such as concentration of nitrogen, phosphorus or water solubles. Decomposition processes have been related to the litter qualities which influence the activities of microbial populations.

But there were rather few studies on the roles of soil microarhropods in the microbial deceomposition processes. Decomposition process of nutrient poor sites proceed through the interaction between the litter qualities and soil animal and microbial popualtions. In the nutrient limited coniferous forests, the indirect effects of soil animals are important in the decomposition processes. Fungal population provides the different colonizing conditions for soil animals in each decomposition stage, and promote the successional changes of soil animals. The roles of soil animals for the decomposition may change in each decomposition stage. In the soils of these forests, Collembola and Cryptostigmata are dominant groups of soil arthropods, they may influence the microorganism populations through the mechanisms of comminution, grazing and dispersal. The indirect effects of Collembola and Cryptostigmata are different with the conditions of litter, because the effects are not the mechanisms only through the soil animals, but through the interactions between litter quality, microorganisms and soil animals. Thus, long-term joint studies between litter, micro-flora and microarthropods in decomposition processes are required to reveal the complete decomposition processes of leaf litter, especially in mor and moder humus forms where decomposition may be a slow process (Staaf & Berg 1982; Edmonds 1984; Takeda 1988, 1995).

Objectives of the study

The objectives of this thesis are to show the pattern of pine needle decomposition in terms of nutrient dynamics (C, N, P, K, Mg, Ca) and fungal and soil animal population dynamics over a four year period in a coniferous forest soil with a moder humus form, and to interpret the successional changes of Collembola and Cryptostigmata during the decomposition processes of pine needle litter. A further aim of this thesis is to assess the indirect roles of arthropods in each decomposition phase of Pinus densiflora litter.

In this thesis, the successional changes of soil animals during longer term decomposition processes are investigated in relation to decomposing litter. The litter condition in each decomposition stage are expressed by the nutrient concentration and fungal abundances in the decomposing litter. The nutrient concentration of litter changed through the activities of fungi, thus nutrient concentrations of litter may reflect the conditions of fungal populations. Fungi might also be one of the main foods for the soil animals. Therefore fungal conditions may reflect the colonizing conditions and food

status for the soil animals. Then, the changes of community structures of Collembola and Cryptostigmata during the decomposition processes are related to the litter conditions such as litter quality and fungal abundances. The feeding habits of Collembola and Cryptostigmata species are also investigated to show the indirect roles of soil animals in the decomposition processes of litter.

2. Study area

The study was carried out in a natural forest of Japanese red pine (*Pinus densiflora* Sieb.et Zucc) mixed with *Chamaecyparis obtusa* Endle at Kamigamo Experimental Forest Station of Kyoto University, about 12 km north of Kyoto city (35.04'N and 135.43'E). The shrub layer was mainly dominated by *Pieris japonica* D. Don, *Euria japonica* Thumb. and *Lyonia ellipica* Okumura. A study plot of 10 m x 10 m in area was laid out in the pine forest. Meteorological records were obtained from the station. Mean annual precipitation and evaporation were 1,678 mm and 985 mm respectively. Fig 2.1 shows the monthly average temperature and precipitation in study site. The surface litter layer often dries out in May and mid summer. The soil humus form in this study area is a Moder with a poorly developed mineral soil horizon (A) which is about 1 cm in thickness. The A_0 layer consists of L, F and H layers, ranging from 2 to 5 cm in thickness. The transition between the H and A layers is indistinct, but the boundary between the A and B layers is very sharp. The A_0 layer is the main habitat for the soil microarthropods in this study area (Takeda 1976). Litter fall was measured in this plot over a 3 year period from January 1979 to December 1981. Annual litter fall ranged from 4137 to 4960 kg x ha^{-1} with a mean of 4573 kg x ha^{-1} and was concentrated in the winter period from November to January in every year. Among the total litter fall, pine needle litter ranged from 1790 to 2160 x ha^{-1} with a mean of 2381 x ha^{-1}. Litter fall showed a clear seasonal pattern with a peak in winter period from November to January.

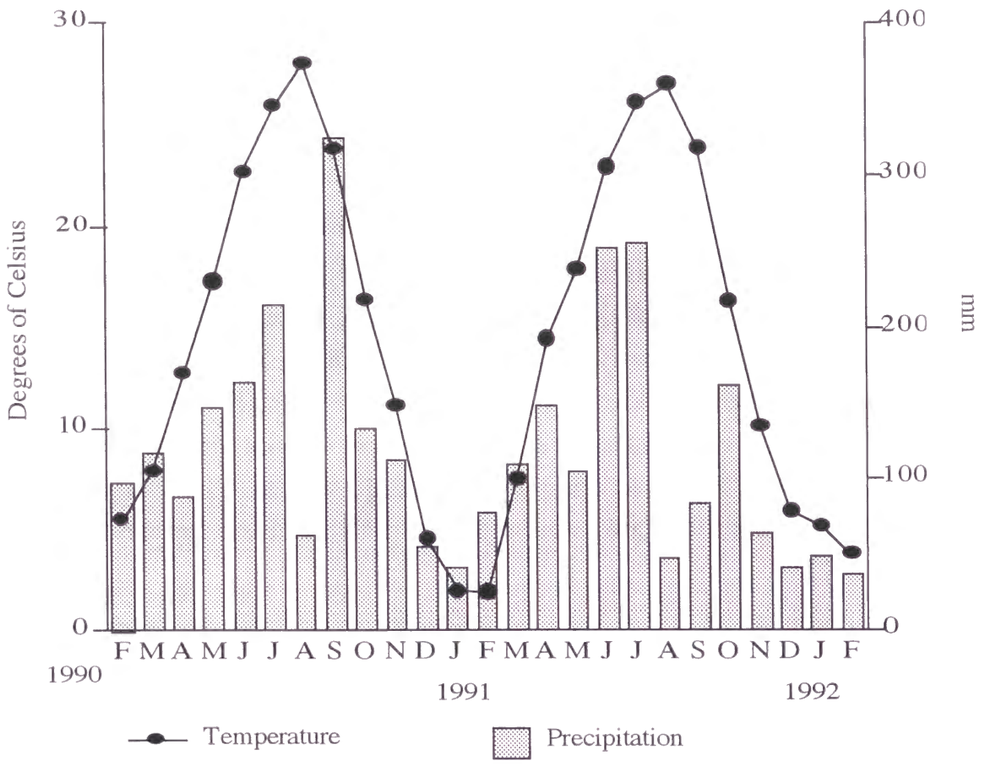


Fig.2. 1. Monthly average temperature and precipitation in study site during first 2 years in studying periods (Kamigamo experimental forest, Kyoto, Japan)

3. Decomposition processes of pine needles in the study area

In the soil system, plant litter is a main resource for the organization of soil organisms and provides both the food and habitat for soil organisms (Takeda 1994, 1996). Abiotic and biotic conditions of plant litter change through the decomposition. Abiotic dynamics include the changes in temperature or humidity. Especially humidity is one of the most important limiting factors for the various soil animals (Wallwork 1970, Joosse & Veltkamp 1970). Humidity changed with the decomposition processes, i. e. with the depths of organic matter layer. The preference of species for humidity may determine the distribution of the species.

Biotic changes include the conditioning of litter by colonization of microorganisms or the activity of other animals. The microorganisms are the main food for the microphytovorous Collembola and Cryptostigmata. In addition, microorganism activity is a main driving factor of the nutrient concentration of litter. Among nutrients, nitrogen and phosphorus are the essential nutrients for the biosynthesis. Nitrogen dynamics of decomposing litter showed leaching, immobilization and mobilization phases (Berg & Staaf 1981; Takeda 1995) and have been related to the activity of microbial population (Berg & Söderström 1979). Thus, the result of microorganisms activity might change the nutritional conditions of decomposing litter. The nutrient concentration of litter is a useful indicator of microorganisms activities, and be related with the soil animal colonization.

The objectives of this chapter are to relate the changes of litter qualities to the colonization processes of soil animals during the decomposition processes. The changes of litter qualities during decomposition were followed using a litter bag containing pine needle over a four year period in a coniferous forest soil with a moder humus form. The changes of decomposing litter were expressed in terms of colonization of fungi and nutrient dynamics (C, N, P, K, Mg, Ca) of the pine needle litter. In the chapter 5, the characters of litter in each decomposition phase are recognized as the background for the community organization of soil animals and related with a colonization of soil animals in the decomposition phases of Pinus densiflora litter.

Materials and methods

Litter bag methods

Decomposition processes of pine needle litter were studied by a litter bag method (Crossley & Hoglund 1962). Newly fallen needles of *Pinus densiflora* trees were collected from the forest floor in December 1989. Litter bags (each 10 cm x 10 cm in area with a mesh size of 3 mm) were used for the decomposition study. Three grams of air-dried pine needles were placed in each litter bag. This litter mass approximated the litter falls in this study area (Takeda 1988). The litter bags were set out in a 10 m x 10 m study plot divided into 10 subplots each 2 m x 5 m in area. A 1 m x 1 m area was laid out in each subplot to contain 20 litter bags. Litter bags were placed on February 29, 1990. After the removal of newly fallen litter, the litter bags were fastened to the forest floor by metal pins to prevent movement and to ensure a good contact between the litter bags and the organic layers.

Litter bags were collected every 3 months from May 1990 to February 1992 and were collected in February 1993 and 1994. On each sampling occasion, 20 litter bags were collected from the study plot (i.e. 2 litter bags were collected from each sub-plot), returned to the laboratory, and used for the study of soil animal populations, fungal colonization, and chemical analysis of litter.

Chemical analysis of needle litter

After the extraction of soil animals, samples of litter were used for chemical analysis. Samples of initial and decomposing needles were dried at 80 °C to a constant weight and ground in a laboratory mill to pass a 0.5 mm screen. Total nitrogen and carbon of pine needles were measured by automatic gas chromatography (C-N corder, Yanagimoto Co., Japan). After an acid wet oxidation in HNO_3+$HCLO_4$ the following analyses were performed; vanad-yellow method for P, flame photometry for K, atomic absorption for Ca and Mg.

The decomposition rate of needle litter was estimated using the exponential decay model of Olson (1963); $DM/DM_0 = \exp(-kt)$ where k is the decay constant, t is the year, DM_0 = original mass of dry matter, DM = mass of dry matter after a given period. Carbon and nutrient contents of litter after a given period of decomposition were

calculated by the following formula; Remaining mass (percentage) = $C/C_0 \times DM/DM_0 \times 100$, where C_0 = initial concentration of nutrients (N, P, K, Mg, Ca) or C in litter and C = concentration of nutrients or carbon after a given period.

Estimation of hyphal lengths

Fungal abundances were estimated during the decomposition processes of needle litter over a 48 month period. On each sampling occasion, 10 of the 20 litter bags collected were used for the estimation of fungal abundances after extraction of the soil animals. On the sampling occasion of the 3rd and 4th year, 5 of 10 litter bags were used. In this study, both the hyphal lengths on the surface and within the pine needles were estimated in first 2 years. Hyphal lengths of the 36 and 48 months needles were estimated without separating surface and within needles, because of the fragmentation of needle litter advanced. The hyphal lengths on the surface of needle litter were estimated at 3 monthly intervals during the study period, whereas hyphal lengths within the needle litter were estimated on four occasions, i.e. May and November in 1990 and 1991.

To estimate the hyphal lengths both on and in the needle litter, one gram of pine needles was boiled with distilled water for an hour. Then the surfaces of needles were rinsed by an ultrasonic washer to ensure the collection of fungi from the needle surfaces. The rinsed needles were used for the estimation of fungi colonizing in the needles and the rinse water was used for the estimation of fungi colonizing the needle surfaces.

After the rinsing of needles, the rinse water was diluted to 400 cc with distilled water, and further diluted by transferring 100 ml into 300 ml distilled water twice (dilution 16-1). Dispersing the dilution by an electric stirrer, 2 ml of the suspension were pipetted on to a Millipore filter holder containing a membrane filter (MF-Millipore filter 0.8 mm pore size with 47 mm diameter , Millipore Co) (Hanssen et al. 1974). Then, 100 ml of distilled water and 2 ml of fuchsin stain with lactic acid were added. After the staining process of 3 minutes, the stained suspension was drawn through the filter using vacuum suction. After the filtration, the Millipore membrane filter was dried and transferred to a glass microscope slide. The filter was covered with immersion oil (Nikon, clearing agent) and a coverslip was placed over the surface. One membrane filter slide was prepared for each litter bag sample. Hyphal lengths were measured using a microscope with a 10 X 10 grid eyepiece graticule at a magnification of 400 X. Hyphae of forty fields of view were counted per sample and hyphae were traced on a paper using a microscope (400 X) with drawing apparatus (Nikon).

After the collection of surface fungi, the needles were homogenized in 200 ml water with an electric ultra-homogenizer run at 3000 rpm for 3 min. and homogenate was used for the estimation of fungi within the needles. Measurement of hyphal lengths in the needle was carried out as in the case of surface fungal hyphae measurements.

Morphological changes in needle litter were studied using a scanning electron microscope and optical microscope. These studies were qualitative, designed to provide a visual record of microbial colonization on/in needles and animal feeding scars on needles during the decomposition process.

Results

Change in the litter mass and water content during decomposition

Figure 3. 1a shows the changes in weights of pine litter over a 4 year period from February 1990 to February 1994. About a thirty three percent of the original mass remained at the end of experiment. Decomposition rates of pine needles were expressed by the decomposition constant of Olson (1963) (Table 3. 1). The decomposition rates decreased with the field exposed time and were significantly higher in the first one year than in the rest of the experiment periods.

Changes in water contents of pine litter were monitored over a 4 year period and are shown in Fig. 3. 1b. In the first 9 months, water contents ranged from 50 to 60%. Water contents of needle litter increased sharply after the end of the litter fall period in the winter of 1990. Then, water contents of litter ranged from 150-450% through the rest of study period and were maintained by the coverage of newly fallen litter on the litter bag.

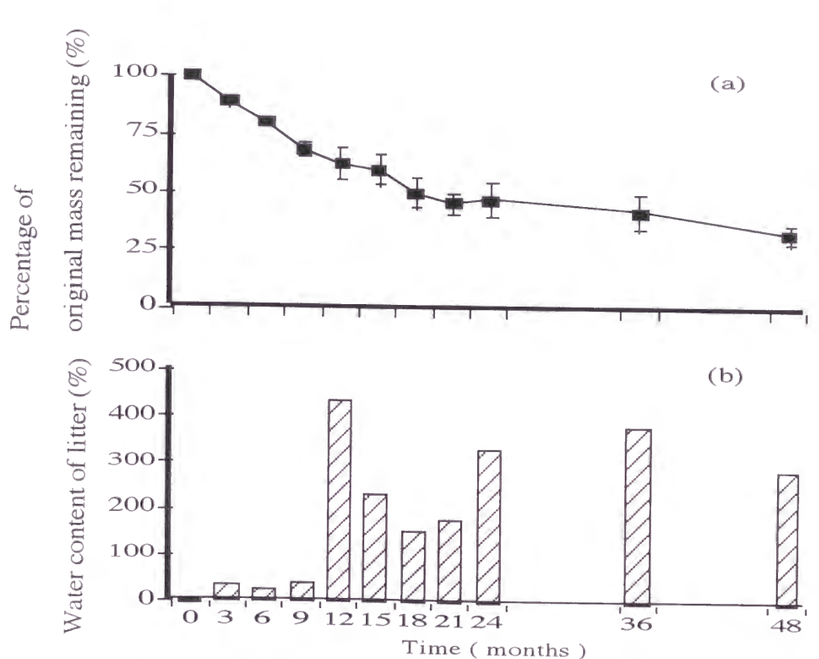


Fig. 3. 1. (a) Percentage of original mass remaining of needles during the decomposition process
(Bars indicate standard deviations.)
(b) Changes in water contents of litter during the study period

Table 3. 1. Decomposition rates for Pinus densiflora needles over a 4 year period

Time (treatment)	Decomposition rate (k)
0-1 year	0.467
0-2 year	0.374
0-3 year	0.288
0-4 year	0.276

Nutrient dynamics in needle litter

Figure 3. 2 shows the changes in carbon and nutrient mass during the study period as the percentages of the initial mass. Changes in carbon mass were similar to those in weight loss. While, the changes in mass of nitrogen and phosphorous showed three phases; (1): leaching loss in the first 3 months in both nitrogen and phosphorous, (2): initial net immobilization during 3 to 9 months in both nitrogen and phosphorous, and (3): the steady-state phase during 9-48 months, no mass change in nitrogen and gradual increase in phosphorous.

In the first leaching phase, nitrogen and phosphorous mass decreased about 7 % and 6 % of the original amounts, respectively. During the initial net immobilization phase, nitrogen and phosphorous mass increased to 145 and 200 % of the original mass, respectively. Finally the nitrogen mass was in steady-state over the rest of the study period. While phosphorus mass was slowly immobilized throughout the steady-state phase.

Potassium mass decreased quickly during the first 3 months and then slowly decreased to 50% of the original mass. Thereafter potassium mass retained about 50% of the original mass throughout the rest of the study period. Magnesium mass rapidly decreased probably due to leaching during the first 3 months. Changes of calcium mass were similar to those of carbon, except with a mass increment during the first 3 months.

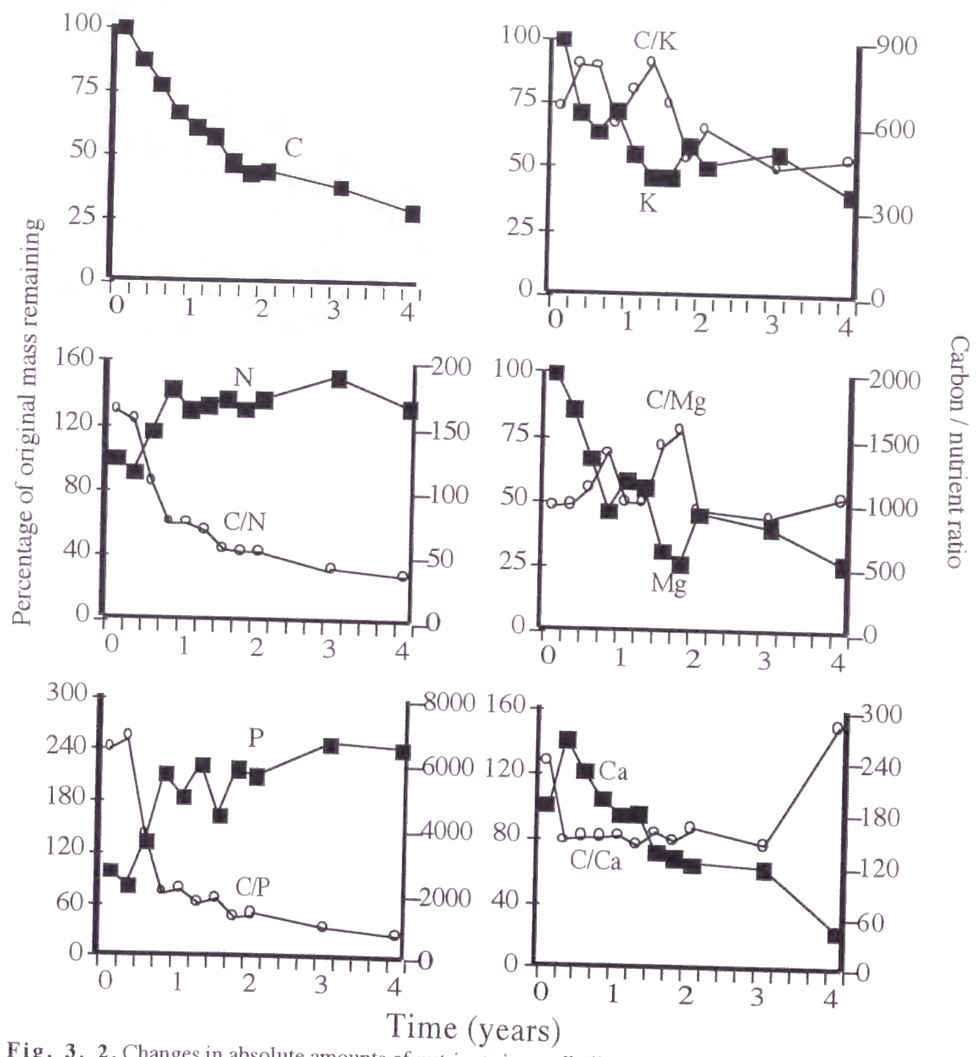


Fig. 3. 2. Changes in absolute amounts of nutrients in needle litter during decomposition (Values are shown as the relative proportion remaining of initial amounts of each nutrients.) and carbon / nutrient ratios of needle litter during decomposition

Changes in Carbon to Nutrient ratios

Figure 3. 2 shows the carbon to nutrient ratios during the decomposition periods. The carbon to nitrogen ratio (C/N) was 162 for the initial needle litter, then decreased to 154 during the leaching phase from 0 to 3 months. During the net immobilization phase from 3 to 9 months, the C/N ratio changed from 154 to 76. Then, the C/N ratio changed gradually from 76 to 36 during 9 to 48 months. The carbon to phosphorous ratio (C/P) decreased quickly during the first 9 months and then slowly decreased through the rest of the study period. The carbon to potassium ratio (C/K) was variable throughout the study period. The carbon to magnesium ratio (C/Mg) was also variable throughout the experimental period and there were no remarkable differences of the ratios between the initial and final litter samples. The carbon to calcium ratio (C/Ca) was steady-state throughout the study period with the exceptions in the initial and final litter samples.

Changes in nutrient concentrations

Figure 3. 3 shows the changes in concentrations of nutrient in relation to accumulated mass loss of pine needles. The concentrations of N and P increased linearly with accumulated mass loss. The correlation coefficients between litter mass loss and concentrations of N and P were positive (Table 3. 2). The results showed a strong retention of N and P in the decomposing litter during the study period. The concentrations of K were decreased in the first 3 months and then increased during the rest of the study period. The coefficient between litter mass loss and concentration of K was positive. The concentrations of Mg and Ca showed no significant correlation with the litter mass losses during the study period.

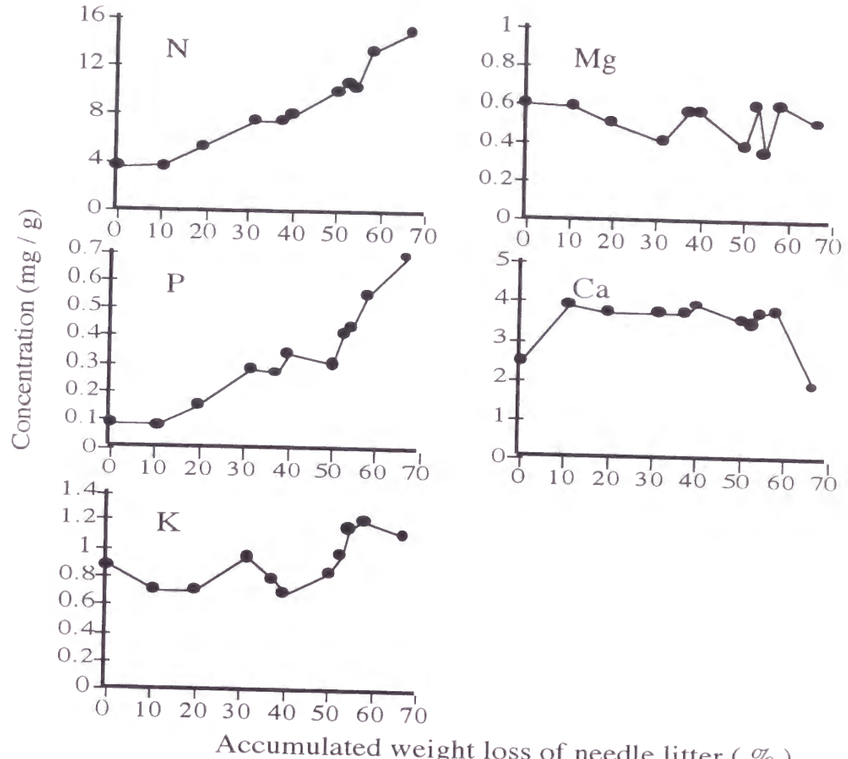


Fig. 3. 3. Changes in concentrations of nutrients in relation to accumulated litter mass loss for needle litter

Table 3. 2. Correlation coefficients for linear relations between accumulated litter mass loss and concentration of some nutrients

Nutrient	Coefficients of correlation
N	0.966***
P	0.934***
K	0.654*
Mg	-0.082
Ca	-0.278

* $p < 0.05$; *** $p < 0.001$.

Changes in fungal abundances on and in the needles

Figure 3. 4 shows the changes in hyphal lengths on the needle surface and in needles and total lengths during decomposition processes. Fungal colonization on the needle surfaces was characterized by three stages as follows; stage 1: growth (3 to 9 months), stage 2: steady-state (9 to 18 months), and stage 3: collapse (21 to 48 months). During stage 1 to 2 , the hyphal lengths on the needle surface were significantly related to the C/N and C/P ratio (for C/N, $p < 0.01$,$r = -0.935$, d.f.=4; for C/P, $p < 0.01$, $r = -0.947$, d.f.=4), and suggesting the immobilization of nitrogen and phosphorus by fungal growths on the litter surface.

The hyphal lengths in the needle increased from 693 m/g at the 3 months to 2694 m/g at the 21 months. Hyphal lengths in the litter increased rapidly during the period from 0 to 9 months as in the case of the surface fungi. Then the increasing rate was low during the rest of the study period. The total hyphal lengths at the 36th and 48th month decreased to about 2000 m/g. It suggests that the 3rd and 4th year were also in the collapse stage of hyphal lengths.

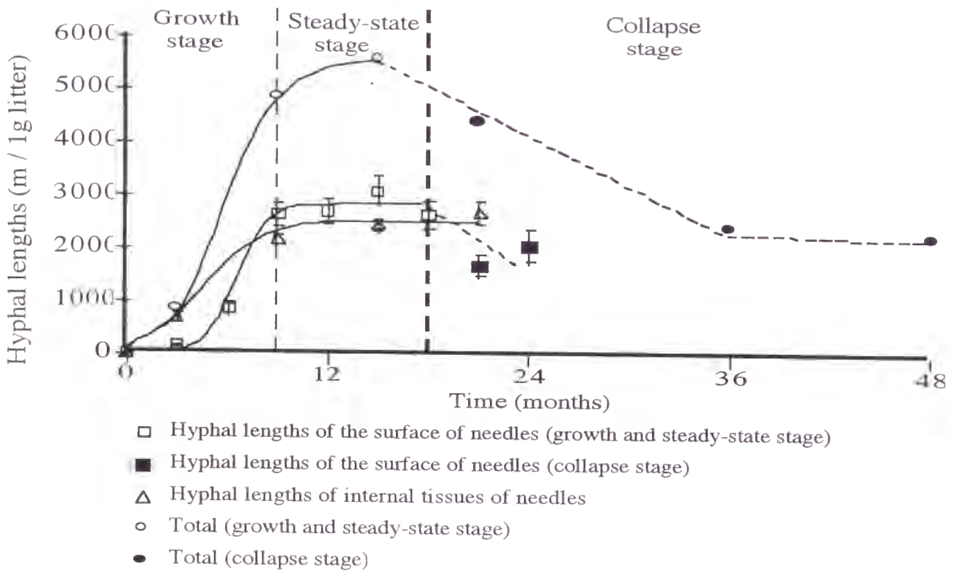
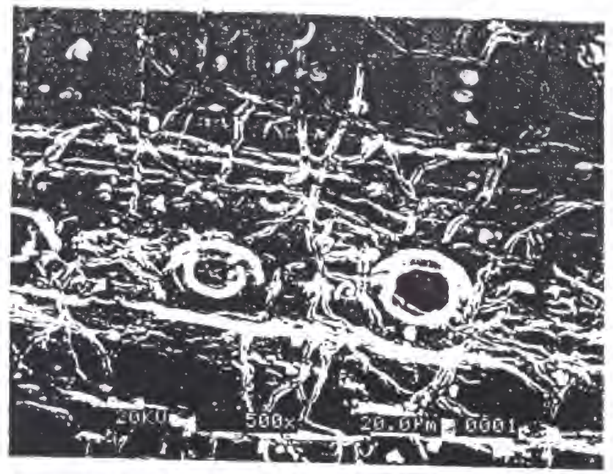


Fig. 3. 4. Changes in the hyphal lengths during 4 years of decomposition
For the 3rd and 4th year samples the hyphae of the surface and internal tissues of needles cannot be separated because of fragmentation.

(a)



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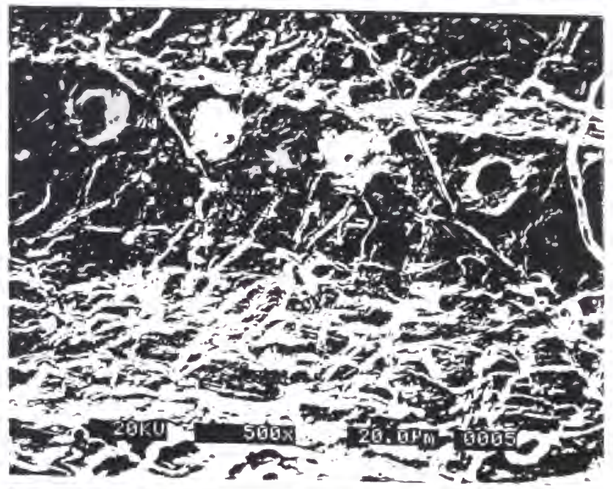

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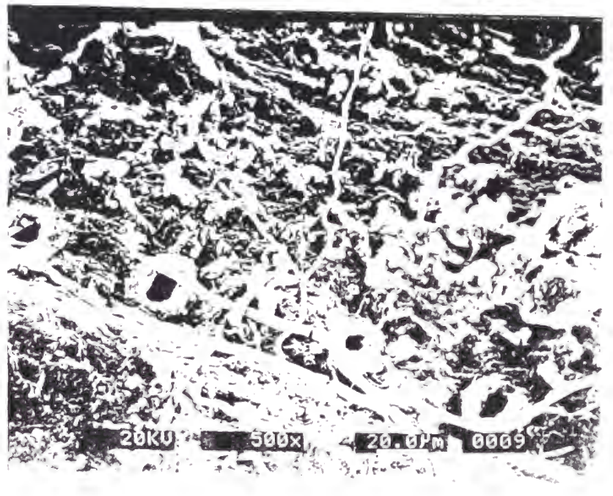


Fig. 3. 5. a. b. c.

(d)

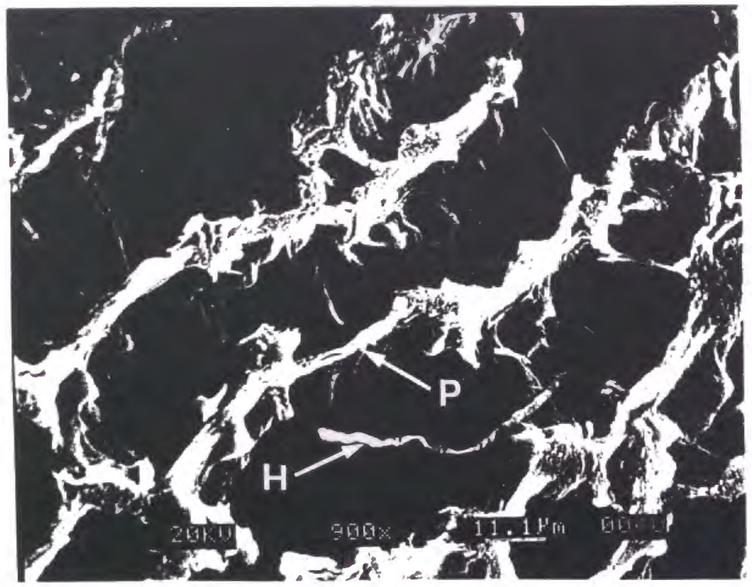


Fig. 3. 5. Morphological changes on the surfaces of needles in the litter using a scanning electron microscope (SEM) during the decomposition process. (a) Surface of needle at the 3rd month. (b) Surface of needle at the 12th month. (c) Surface of needle at the 24th month. (d) The fungi colonizing into the palisade tissues of the needles

H; Hypha of fungi, P; Cell wall of the palisade cell

Fig. 3.5 (a, b, c) revealed the decomposition processes occurring on the pine needles during the decomposition observed by SEM. Needles remained intact during the leaching and immobilization phase, but with the advance of decomposition the surface of needles was colonized by fungi. These fungi colonized the wax and epidermis layers of needles during the immobilization phase. After one year, the surface of needles was completely covered by the fungal mycelium, and the wax and epidermis were converted into fungal biomass. Figure 3. 5 (d) shows the fungi colonizing into the palisade tissues of the needles observed by SEM.

Discussion

Changes in litter weights during the decomposition

Table 3. 3 shows the character of litter in each decomposition phase in terms of fungal conditions, hyphal lengths and carbon and nutrient status. Decomposition processes consisted of two phases. The decomposition rates of pine needles decreased with the field exposed time and were significantly higher in the early decomposition phase than in the late decomposition phase. Long term study of coniferous litter showed a retarded decomposition rate during the late decomposition phase (Berg et al. 1982; Takeda 1988, 1995). In the late decomposition phase, the decreases in decomposition rates with exposed periods have been explained by the increases of refractory components in the decomposing litter (Berg and Ågren 1984). Berg (1986) suggested that decomposition of litter may be divided into at least two phases. In the first phase soluble substances and non-lignified carbohydrates (cellulose and hemicellulose) are decomposed by saprotrophic fungi. In the late decomposition phase, on the other hand, primarily lignin and lignified cellulose remain.

Table 3. 3. Characteristics of two decomposition phases, i.e. the early phase from 3 to 18 month and the late phase from 21 to 48 months, in terms of carbon and nutrient states (N, P) and fungal abundances.

Decomposition phase	early phase		late phase
Time (months)	3-9	12-18	21-48
Fungal condition	growth stage	steady-state stage	collapse stage
Hyphal lengths (m / g. d. wt. of litter)	2848 (858-4837)	5557	3022 (2247-4394)
Nitrogen and phosphorus state	leaching rapid immobilization	steady-state	steady-state
Carbon loss rate (mg C / month)	57	37	8.5
C/N ratio	75.9-155	56-75.8	35.9-53.7

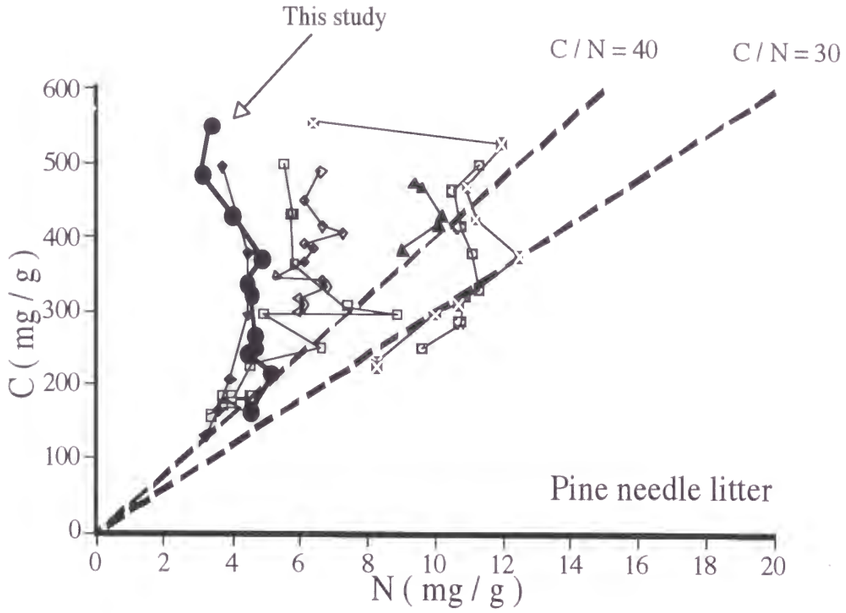
Changes in nutrient mass during the decomposition

Nutrient dynamics of decomposing litter were categorized into three types. The first type was characterized by the leaching loss in the first 3 months of decomposition processes. Potassium showed such a type. The second type showed changes in their amounts similar to those in needle weights, as in the cases of Ca and Mg. Nitrogen and phosphorous showed third type, which was characterized by the increases of the concentrations and absolute amounts during decomposition. This type of the nutrient such as nitrogen and phosphorous has been suggested to limit the growth of microbial populations in some studies (Staaf and Berg 1982; Berg & Söderström 1979; Bååth & Söderström 1979; Ausmus et al. 1976). During the pine needle decomposition processes, the leaching, accumulation, final release phase of nutrients are distinguished for the limiting nutrients such as N and P (Berg & Staaf 1981). In this study, nitrogen and phosphorous followed the leaching, immobilization and steady-state phase. But no mobilization of N and P occurred even in the end of this experiment.

The relation of litter weight and C/N changes

Figure 3. 6 shows the changes in amounts of C and N during the decomposition of pine and another coniferous needle litter. In this figure, the data showing the nitrogen accumulating and releasing phase in the decomposition of needles are chosen for the analysis (see, legend of Fig 3. 6). Fig. 3.6 indicates that amounts of nitrogen increased with decreasing of amounts of carbon in the early phase of decomposition. When the C/N ratio of decomposing needles reaches the ratios of C /N between 30 and 40 (pine), 20 and 40 (other conifer), amounts of carbon and nitrogen in litter bags decreased, while the weight loss occurred with a constant C/N ratio. Exceptionally in some case studies, some litter shows nitrogen release with a high C/N ratio, i.e. over the C/N = 40. Aber et al.(1990) investigated N dynamics in decomposing litter and provided a model of nitrogen dynamics. This model consists of two-phases N dynamics. In an early phase, the concentration of N increased linearly to accumulated mass loss, whereas in a later phase no changes in nitrogen concentration took place.

Figure 3. 7 shows the changes in C/N with time for some long term decomposition studies. The changes in C/N ratios during the decomposition are well represented by asymptotic curves with two parameters. Regardless of the initial C/N ratios, C/N ratios converge to a constant value, i.e. C/N = 30 in coniferous litter, C/N = 40 in pinus litter. This model also well represented the immobilization and mobilization processes of nitrogen with the carbon dynamics. So the decomposing pine litter apparently provides two resource conditions for the colonization of soil animals.



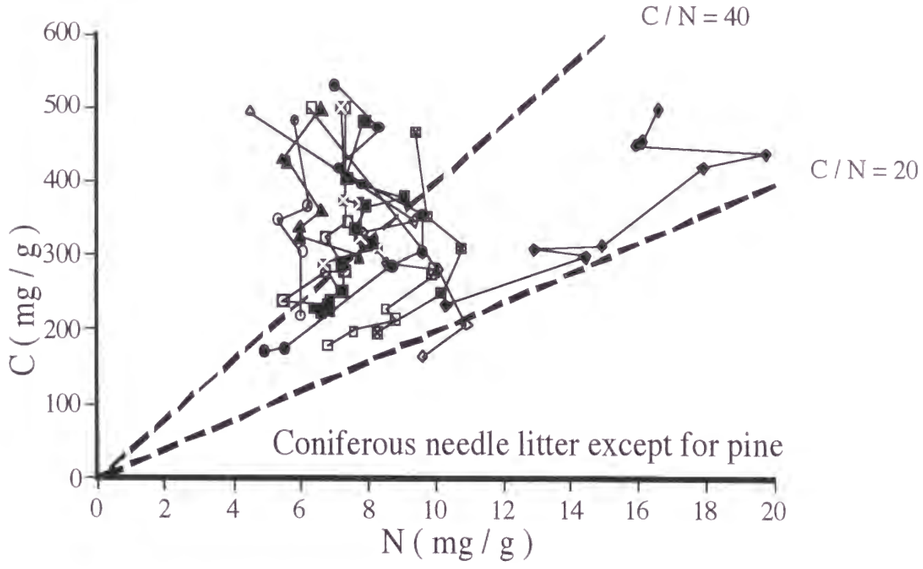
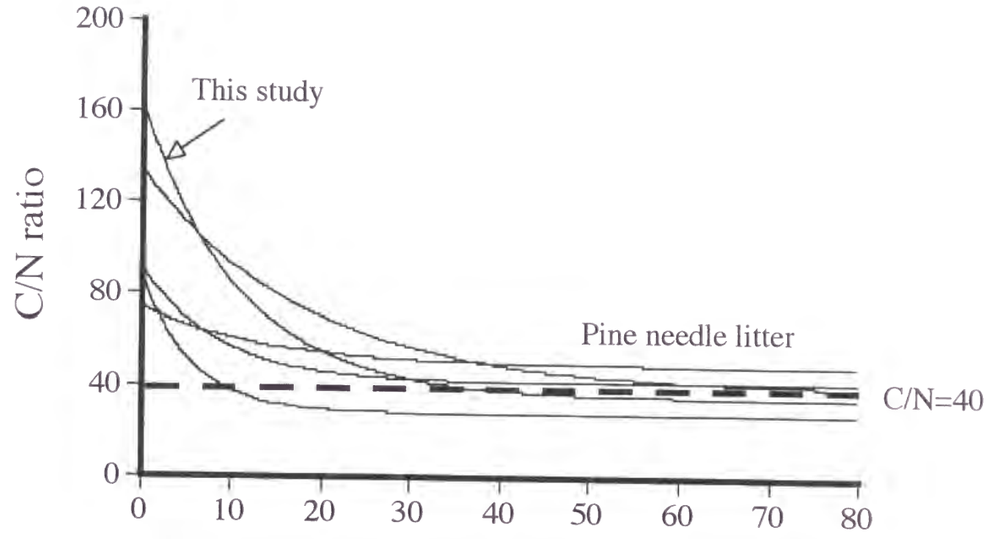


Fig. 3. 6. C/N dynamics in relation to carbon and nitrogen dynamics of some decomposition studies (a) Dynamics of pine needle litters (b) Coniferous needle litters except for pine

Data from Maclean and Wein (1978), Rustad & Cronan (1988), Rustad (1994), Bockheim and Leide (1986), Will (1968), Klemmedson (1985), Staaf and Berg (1982), Stohlgren (1988), Edmonds (1980, 1984), McClaugherty et. al.(1985), Tietema (1993), Takeda (1995). An average of 50% carbon was assumed for the data of studies which have not shown the value of Carbon content.



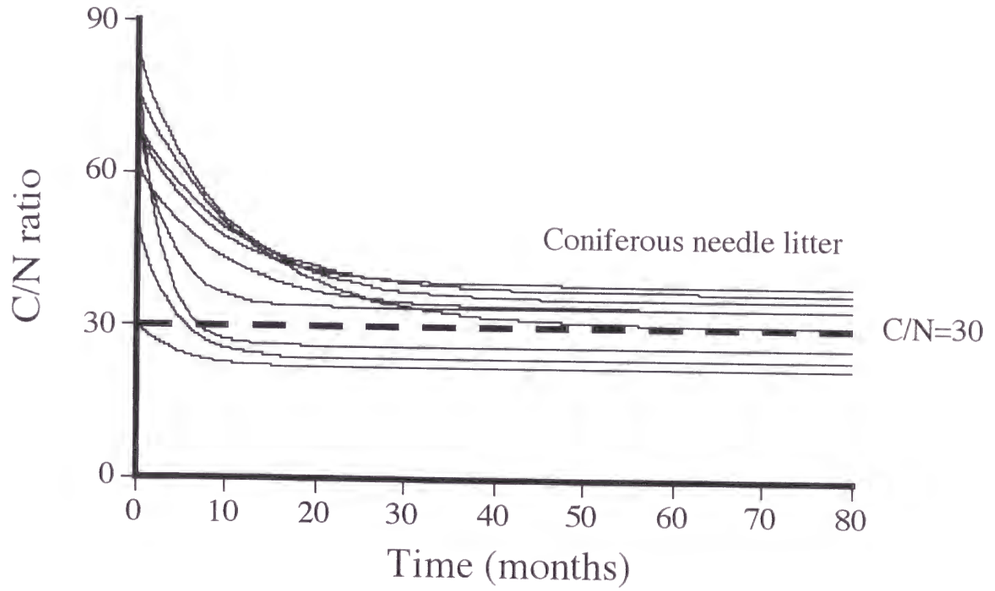


Fig. 3. 7 Changes in C/N ratios of the litters against time in some studies
The formula of the lines is $Y = a + \exp(-c \times X) \times (C_{(i)} - a)$ where X = exposed time, Y = C/N ratio and $C_{(i)}$ is an initial C/N ratio. (a) Pine needles (b)Coniferous needle litter except for pine.

Data from Rustad & Cronan (1988), Rustad (1994), Will (1968), Klemmedson (1985), Staaf and Berg (1982), Stohlgren (1980), Edmonds (1980, 1984), Tietema (1993), Takeda (1995)

The dynamics of limited nutrients (nitrogen, phosphorus) have been related to the nutrients and carbon utilization by the microbial populations (Berg & Staaf 1981). In this study, the fungal colonization patterns were characterized by the three stages as follows: 1) growth stage during 3 to 9 months, 2) steady-state stage during 12-18 months, and 3) collapse stage during 21 to 48 months.

Table 3. 3 shows that fungal populations contributed to the net immobilization of both nitrogen and phosphorus during the growth stage. Nitrogen and phosphorous were strongly immobilized in the growth stage, during which immobilization rates exceeded the mobilization rates of nutrients. During the steady-state stage, N and P amounts remained steady-state, while the carbon mobilization still continued. During this stage, immobilization rates of nutrients were balanced to the mobilization rates. The carbon loss rate decreased during the collapse stage, fungal population reduced their abundances but the nitrogen and phosphorus were well retained in the litter until the end of experiments. Thus, the immobilization and mobilization of N and P were balanced. In this stage, the decomposition process is controlled by the factors that influences the decomposition rate of lignin (Berg 1986).

It is concluded that two decomposition phases (i. e. early and late phase) produced the different colonizing conditions for the soil animals. In the early decomposition phase fungal conditions were in growth stage or in steady state, while in late decomposition phase fungal conditions were in collapse stage. The diffferent fungal conditions might influence the colonaization of microphytovorous animals. In the late decomposition phase the litter might be composed of retarded part of the original litter and the part processed by microorganisms or animals (ex. dead body of fungi or animal feaces). In this phase, the litter in the bags was processed slowly. The retarded part of litter is difficult to utilize for the microorganisms or animals, and the part already processed might be recycled by the decomposers. The detritivorous animals might depend on the recycling of organic matter.

4. Succession of soil animals during the decomposition of pine needles

In the Chapter 3, it is concluded that two decomposition phases (i. e. early and late phase) provided the different colonizing conditions for the soil animals. These different conditions were characterized by the fungal abundances and nutrient concentration of the decomposing litter. In the soil system, plant litter is a main resource for the organization of soil organisms and is changed through the interactions between microbial and animal decomposers. Decomposing litter provides both food and habitat resources for soil organisms. Some studies (Metz and Farrier 1969, Anderson 1975; Hågvar & Kjøndal 1981; Takeda 1988) followed the colonization processes of soil animals using litter bag methods, but were not related with the conditions of decomposing litter. Successional changes of soil animals are responses of individual species to the resource conditions during decomposition processes. Thus joint studies of soil animal populations and resource dynamics of decomposing litter are important for the interpretation of successional patterns of soil animals.

This chapter concerns the successional changes in the microarthropod fauna (Collembola and Cryptostigmata) during decomposition. These groups are very abundant in forest soil and participated in all stages of decomposition. Because of their high abundances and species richness, they are suitable for the study of zoological succession during various decomposition phases. The information about these animals is important to understand the role of soil animals in the recycling of plant nutrients. Collembola and Cryptostigmata have been recognized to occupy similar niches in decomposition processes, because these two taxa are detritivorous or fungivorous. Most of the studies at species level investigated the colonization process either Collembola (Takeda 1995) or Cryptostigmata (Metz and Farrier 1969, Anderson 1975). Hågvar & Kjøndal (1981) reported the colonization process of both taxa, but they did not comment on the difference of the two taxa. Comparative studies of organization of the two taxa should be made to understand the colonization characters of these two taxa.

The objective of this chapter is to show the community structure of Collembola and Cryptostigmata in each decomposition phase with different conditions. Community structures of Collembola and Cryptostigmata during the decomposition of pine needle litter are compared using various community indices.

Materials and Methods

Soil animal populations

Changes in soil animal populations were studied by litter bag methods. On each sampling occasion, twenty litter bag samples were collected in the first 2 year period and were used for the estimation of soil animal populations. On the sampling occasions of the 3rd and 4th years, 10 and 8 litter bags were collected respectively. Soil animals in the litter bags were extracted by a modified Tullgren funnel at a constant temperature condition of 35 °C in a cabinet for 3 days. Animals were collected in 99% ethanol. Identification, counting and measurements of soil animals were carried out under a binocular microscope with a magnification of 400 X. Collembola and Cryptostigmata (adult stages) were classified into species.

Statistical analysis

Community structure. Community structure of Collembola and Cryptostigmata is expressed by the following parameters: total number of individuals, diversity, species richness and evenness. Community diversity was expressed by the Shannon-Wiener function as follows;

$$H' = \sum_{i=1}^{S} p_i \ln p_i$$

where S is the number of species collected from the litter bags, P_i is the percentage of i th species. Species richness was expressed by the number of species collected in each sample.

Evenness was estimated using Pielou's index (Pielou 1966);

$$J = \frac{H'}{\log_2 S}$$

this value is unity when component species show completely even distribution.

The succession index. In this study, the succession trends of species were quantified by the following two indices. The succession index (M) and succession deviation (S) were

calculated by the formula of Usher (1970) used for the vertical distribution of collembolan species;

$$M = \frac{\sum_{i=1}^{10} t_i n_i}{N}$$

$$S = \sqrt{\left\{ \frac{\sum_{i=1}^{10} n_i (t_i - M)^2}{N} \right\}}$$

where M is the succession index for a given species, and is thus a statistic which reflects the colonization time during the decomposition, *ti* is the months from the start of the experiment at ith sampling, *ni* is the abundance for a given species at the ith sampling. N is the total abundance of a species through the experiment. S is the succession deviation for a given species.

Similarity of species composition among communities at different sampling times. Similarity of species composition betwwen communities at different sampling times was examined using Pianka's α (Pianka 1973), which is expressed by the following formula;

$$\alpha_{1,2} = \frac{\sum_{i=1}^{S} p_{1i} p_{2i}}{\sqrt{\sum_{i=1}^{S} p_{1i}^{\,2} \sum_{i=1}^{S} p_{2i}^{\,2}}}$$

where $\alpha_{1,2}$ shows the similarity between community 1 and 2, p_{1i} and p_{2i} is the the proportion of *i*th species in the community 1 and 2 respectively, S is the total number of species. This value is unity when two communities are completely the same in terms of their species composition.

Cluster analysis. Colonization patterns of Collembolan and Cryptostigmata species in the decomposition were classified using cluster analysis. Cluster analysis results in a hierarchical dendrogram showing species-linkages in a criterion similarity . In this study, the group average method was used. Similarity measure in this clustering strategy should be compatible with the arithmetic average (Kobayashi 1991). Then the chord distances (Orlóci 1967) were used.

Niche breadths and Niche overlap. The niche breadths (Levins 1968) of ith species (RB) on the resource j were measured using Levins's formula as follows;

$$B = -\sum_{j=1}^{L} p_{ij} \ln p_{ij}$$

$$RB = B / \ln L$$

where P_{ij} is the percentage of ith species at jth sampling times. L is the numbers of sampling times.

The niche overlap (alpha) (Pianka 1973) between hth species and ith species was calculated by the formula as follows;

$$\alpha_{hi} = \frac{\sum_{j=1}^{L} p_{hj} p_{ij}}{\sqrt{\sum_{j=1}^{L} p_{hj}^{2} \sum_{j=1}^{L} p_{ij}^{2}}}$$

Results

Colonization process of soil animal populations

Table 4. 1 shows the relative abundances of soil animal groups in the litter bags. Cryptostigmata(Acari) and Collembola were predominant groups in the litter bag fauna and each accounted for 33.7% and 31.6% of the total animal abundances, respectively.

Table 4. 1. Abundances of soil animals colonizing the litter bags during the study period

Group	Population density (m^{-2})	Standard errors	Relative abundance (%)
Cryptostigmata	4045.5	694.0	33.707
Collembola	3796.0	440.2	31.629
Mesostigmata	1334.8	281.6	11.122
Astigmata	1251.3	295.0	10.426
Prostigmata	938.3	300.1	7.818
Diptera	305.3	55.2	2.544
Thysanoptera	114.0	67.7	0.950
Enchytraeidae	99.5	40.2	0.829
Isoptera	59.0	43.2	0.492
Diplopoda	18.8	9.5	0.157
Coccoidea	6.5	5.2	0.054
Coleoptera	4.5	2.1	0.037
Araneae	4.5	2.1	0.037
Lepidoptera	4.5	2.7	0.037
Pseudoscorpiones	4.0	1.3	0.033
Amphipoda	3.5	2.6	0.029
Chilopoda	3.0	2.1	0.025
Symphyla	2.3	1.4	0.019
Pauropoda	2.0	1.2	0.017
Protura	1.5	1.1	0.012
Opiliones	1.0	0.7	0.008
Hymenoptera	1.0	0.7	0.008
Isopoda	0.5	0.5	0.004
Haprotaxida	0.5	0.5	0.004
Total	12001.8		

Figure 4. 1 shows the changes in the densities of soil animal groups during the study period. Densities of soil animals were expressed by the number of individuals per gram of pine litter. The densities of total soil animals increased during the first 15 months and attained a maximum of 115 individuals per gram in the 21 month litter bags. Then the densities decreased to about 85 individuals and were in steady-state throughout the rest of the study period.

The densities of Collembola were 20 individuals per gram even at the 3rd month and decreased at the 6th month because of summer drought in 1992. Then the densities rapidly increased to a maximum of 39 individuals at 21 months. During the rest of the study period, the collembolan densities were about 20 individuals per gram.

The densities of Cryptostigmata were low in the 3 and 6 month samples and then rapidly increased until the first peak at 15 months. After the peak density, Cryptostigmata decreased during a 12 month period. The densities of Cryptostigmata increased from 24 months to the end of the study period. Mesostigmata and Astigmata were later colonizers compared to Collembola. In Prostigmata, the density showed a peak in the 6-months litter bags.

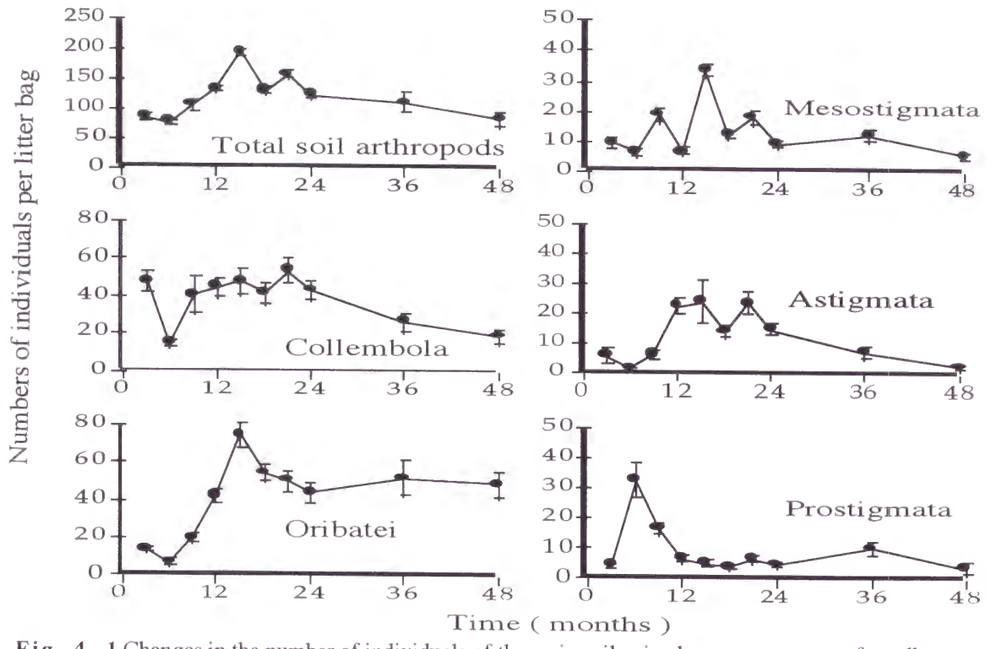


Fig. 4. 1 Changes in the number of individuals of the main soil animal groups per gram of needle litter
Bars indicate standard errors.

Abundance of Collembola and Cryptostigmata species in litter bags

Fig. 4. 2 shows the species rank-abundance curves of Collembola and Cryptostigmata (adult stages) species collected from the litter bags over the 4 year period.

The collembolan community consisted of 29species, i.e., 4 dominant species (over 10% of the total population), 8 rare species (0.5-10%) and 17 very rare species (less than 0.5%). *Folsomia octoculata* is the most dominant species, and accounted for 36% of the total collembolan population. *Tetracanthella sylvatica*, *Onychiurus flavescens* and *Tomocerus varius* were also dominant species and accounted for more than 10% of total collembolan abundance. These four species accounted for 76% of total populations.

The Cryptostigmata community consisted of 70 species, i.e., only one dominant species (over 10%), 26 rare species (0.5-10%) and 43 very rare species (less than 0.5%). *Tectocepheus velatus* is the most dominant species, and accounted for 17% of the total Cryptostigmata population. The abundance of the Cryptostigmata species gradually decreased with the rank of the abundance of the species.

In short, the collembolan community was dominated by few dominant species, while the Cryptostigmata community consisted of many species with relatively similar abundances.

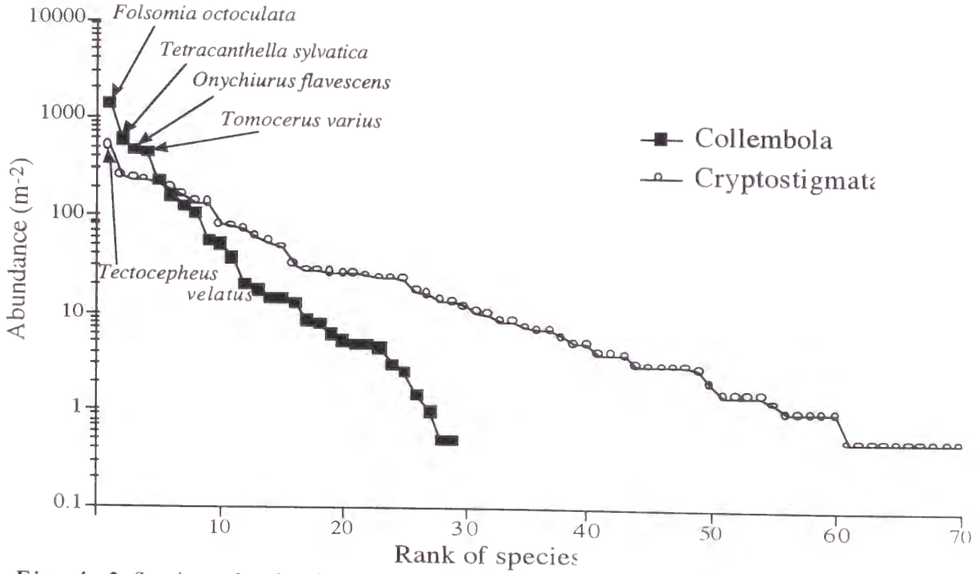


Fig. 4. 2. Species rank - abundance curves of Collembolan and Cryptostigmata(adult) communities colonizing the litter bags during the study period. The abundances are shown as average density collected from the litter bags over a 4 year period

Changes in diversity, evenness and species richness of the Collembola and Cryptostigmata community in the litter bags are shown in Fig. 4. 3.

Diversity of the collembolan community showed seasonal variations with low values in winter. Diversity of the collembolan community showed annual changes and significantly correlated with species richness (Spearmann rank correlation, $r = 0.72$, $p < 0.05$) but not with evenness component. Diversity of Cryptostigmata was higher than that of Collembola throughout the study period. In the first year, seasonal changes in Cryptostigmata diversities showed a similar trend to that of Collembola. But annual changes in Cryptostigmata diversities were different from those for Collembola. Diversity of the Cryptostigmata community was significantly correlated with species richness and with evenness component, but higher correlation was obtained for species richness (Spearmann rank correlation, species richness; $r = 0.83$, $p < 0.01$, evenness; $r = 0.624$, $p < 0.05$).

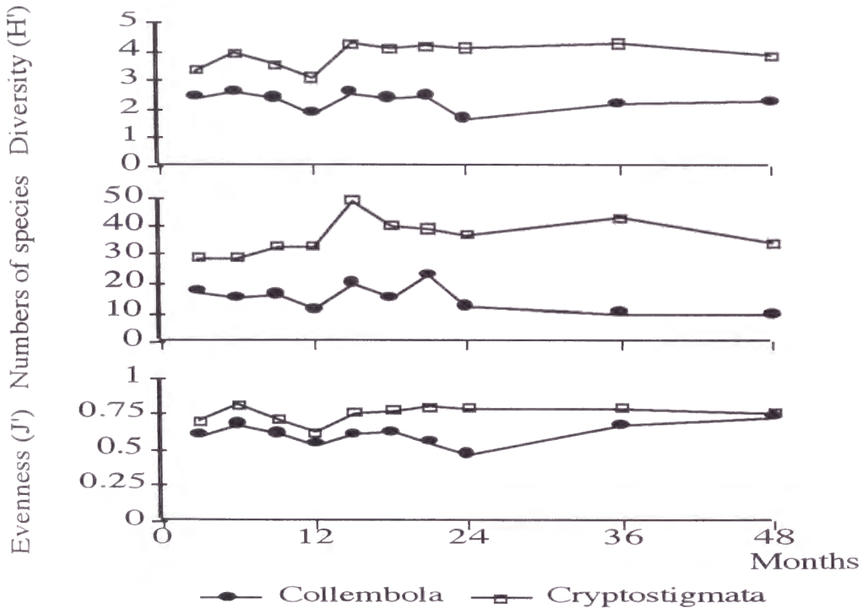


Fig. 4. 3. Changes in parameters of Collembola and Cryptostigmata (adult) communities; i.e.
diversity index (H'), evenness(J') and species richness (number of species collected at each sampling occasion) in litter bags

A successional trend was observed in the species composition during the study period, and the similarities of colonization pattern of species were examined by cluster analysis (Fig. 4. 4 a, b).

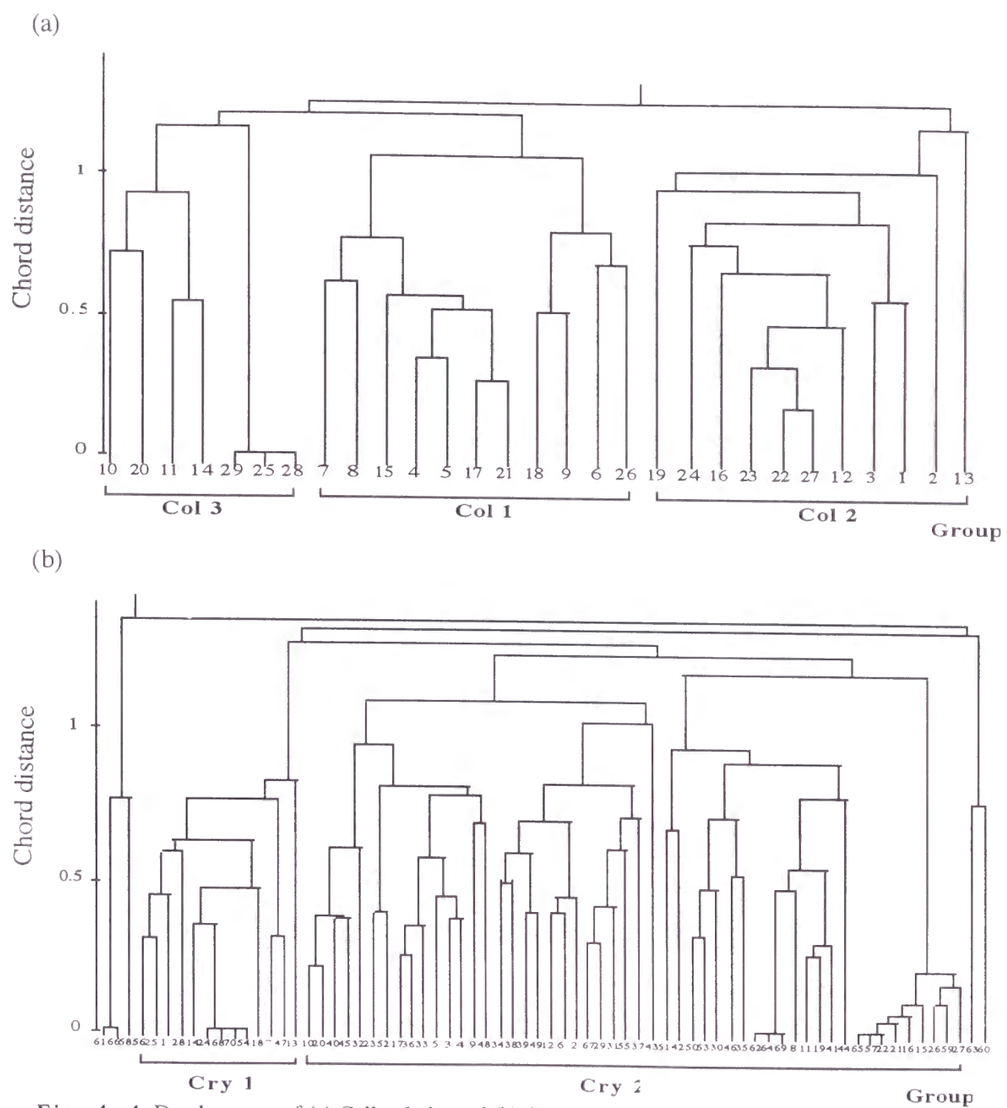
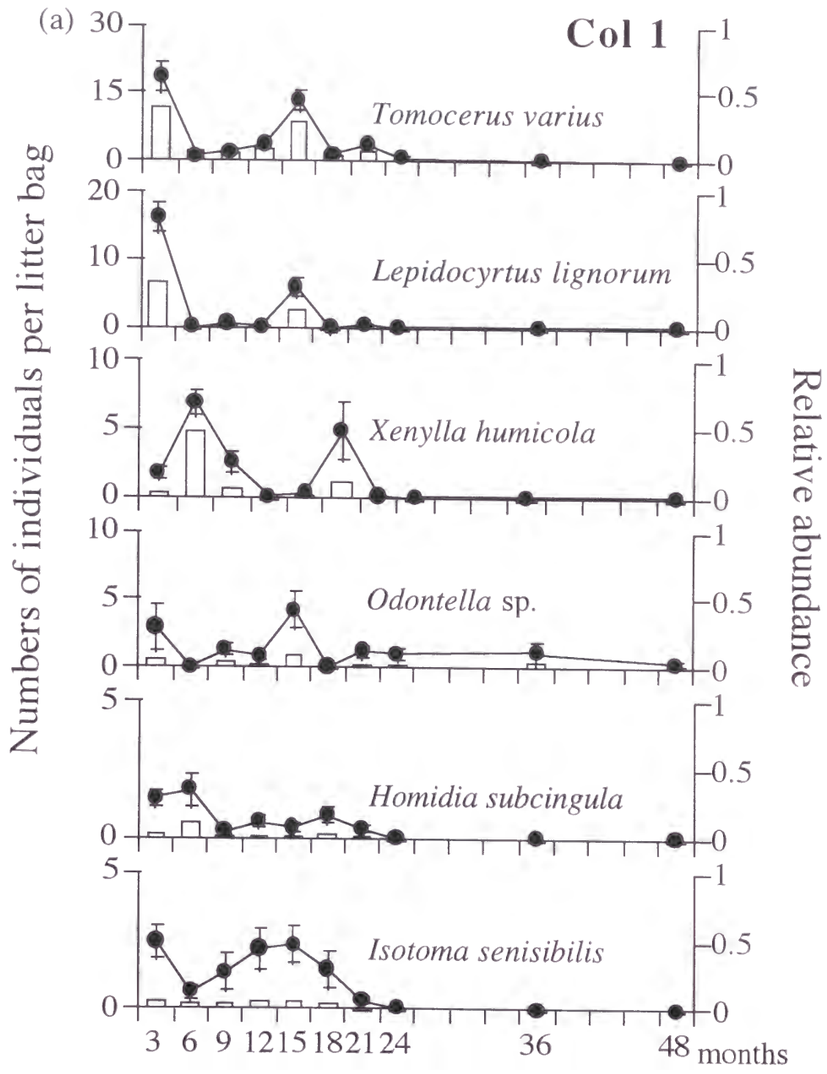


Fig. 4. 4. Dendrograms of (a) Collembola and (b) Cryptostigmata species by the pair-group method using arithmetic averages with chord distance based on colonization time. Numbers indicate species' rank of abundance in each community. Groups identified are depicted by brackets

In the collembolan community, three large groups are identified. The groups were termed Col 1, 2 and 3 in the order of colonization time. Fig. 4. 5a, b and c show the changes in densities of main collembolan species in each groups. Col 1 consisted of the early colonizing species. They mainly consisted of surface dwelling species, such as *Tomocerus varius*, *Lepidocyrtus lignorum*, *Homidia subcingula*, *Isotoma sensibilis*, *Xenylla humicola* and *Odontella* sp.. Col 2 consisted of the late colonizing species, *F. octoculata*, *O. flavescens, Oncopodura crascicornis and Tetracanthella sylvatica*, and these species increased their densities with the advance of decomposition. Col 3 consisted of the eu-edaphic species, such as*Tullbergia yosii* and *Megalothorax minimus*.

In the Cryptostigmata community, two large groups were identified. The groups were termed Cry 1 and 2 in the order of colonization time. Fig. 4. 6a and b show the changes in densities of the main Cryptostigmata species in each group. Cry 1 consisted of intermediate colonizers,*T. velatus*, *Fissicepheus clavatus* and *Brachychthonius elsosneadensis*. The densities of Cry 1 began to increase after 12 months, and decreased after 24 months. Cry 2 consisted of late colonizers (*Hermannia kanoi*, *Hoplophthiracarus pavidus*, *Suctobelba* sp.1, *Suctobelba* sp.2, *Oppiella nova*, *Goyoppia sagami* and *Brachychthonius hungaricus*). The densities of Cry 2 began to increase after 12 months and remained for 36 and 48 months.



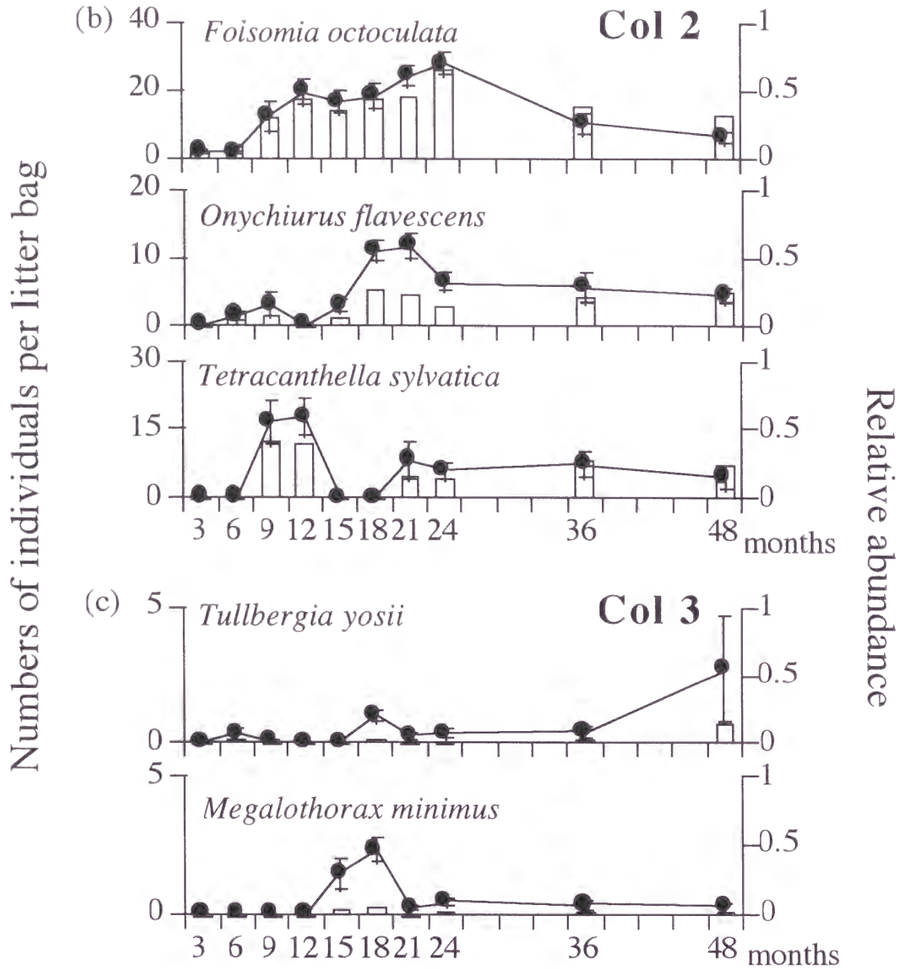


Fig. 4. 5. Colonization patterns of the main collembolan species during the decomposition of litter over a 4 year period. Bars indicate the standard errors, and columns indicate relative abundance of total collembolan abundance. According to the successional trends, collembolan species are classified into 3 groups, i.e., (a) Col 1 consist of the early colonizing species, (b) Col 2 consist of the late colonizing species, (c) Col 3 consist of the true edaphic species

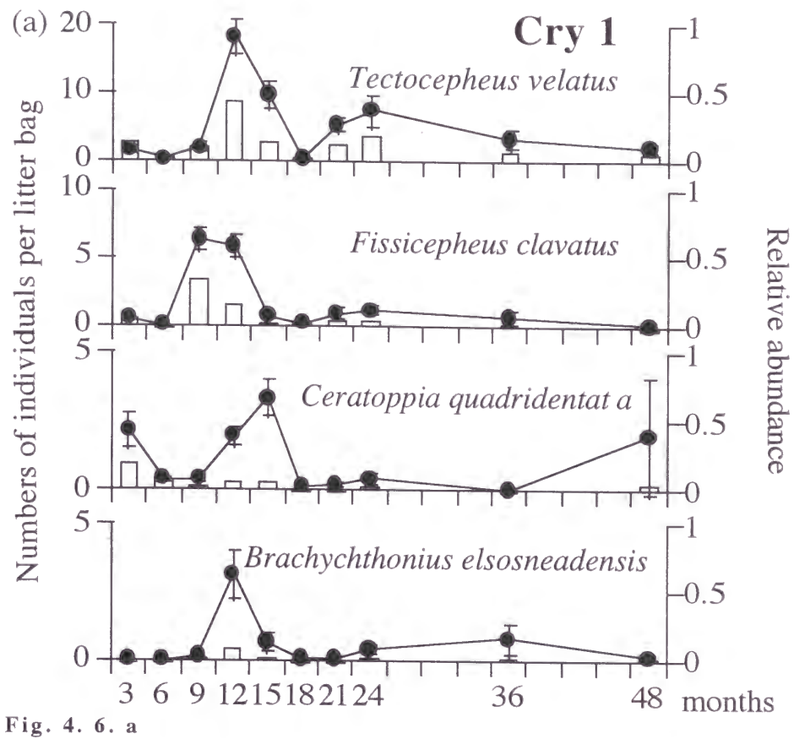


Fig. 4. 6. a

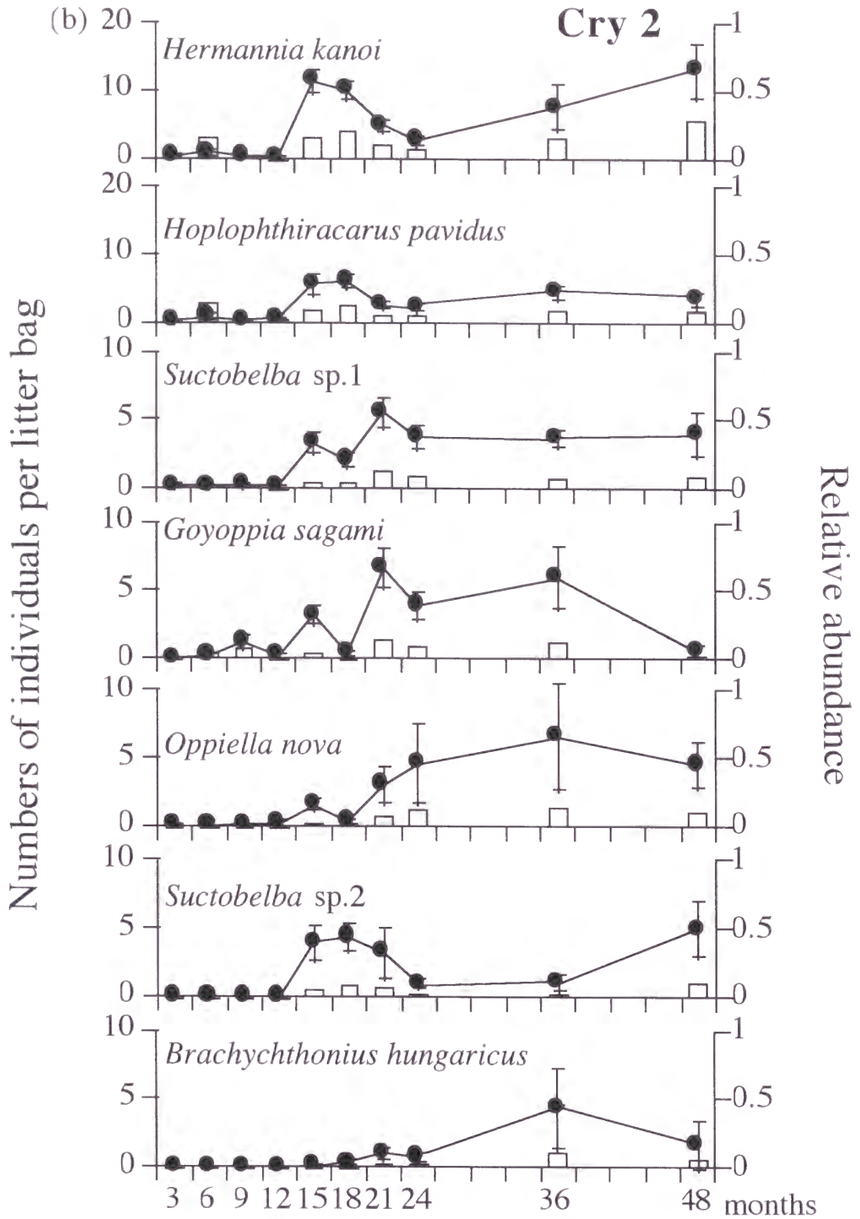


Fig. 4. 6. Colonization patterns of Cryptostigmata (adult stage) species during the decomposition of litter over a 4 year period. Bars indicate the standard errors, and columns indicate relative abundance of total Cryptostigmata abundance. According to the successional trends, Cryptostigmata species are classified into 2 subgroups, i.e. (a) Cry 1, Intermediate, (b) Cry 2, True late colonizers

The succession index was calculated for these species comprising more than 5 individuals during the study period. The succession index of species indicates the center of gravity of colonization time for them. Table 4. 2 a, b show the succession index (M) of Collembola and Cryptostigmata.

Table 4. 2a. Population density and succession index of Collembola colonizing the litter bags during the study period.

The formula of succession index (M)and succession deviation (S) are given in Materials and Method.

	Population density	Succession Index	
Entomobrya sp.1	9	4.4	4.4
Homidia sp.	8	6.4	5.7
Lepidocyrtus lignorum	232	6.6	5.6
Tomocerus punctatus	5	7.5	7.3
Sminthurinus sp.	15	7.6	5.3
Homidia subcingula	57	9.4	6.0
Xenylla humicola	165	10.0	5.7
Tomocerus varius	444	10.1	6.6
Isotoma sensibilis	108	11.0	5.5
Sminthurus sp.	15	14.6	6.0
Arrhopalites sp.	3	15.0	0
Odontella sp.	128	15.2	7.1
Neanura mandarina	3	16.5	5.9
Lophognathella choreutes	5	17.7	5.7
Lepidocyrtus sp.	6	18.5	9.2
Tetracanthera sylavatica	605	19.2	7.2
Folsomia octoculata	1373	20.1	5.9
Micranurida sp.	5	20.1	1.9
Megalothorax minimus	38	21.7	4.3
Onychiurus flavescens	467	23.4	6.4
Isotoma carpenteri	13	24.2	5.0
Oncopodura crascicornis	20	24.6	6.1
Friesea sp.	18	26.1	10.5
Neanura sanctisebastiani	5	26.9	9.9
Tullbergia yosii	52	35.1	12.1

Table 4. 2b. Population density and succession index of Cryptostigmata colonizing the litter ba during the study period

	Population density	Succession Index	
	(m^{-2})	M (months)	S (months)
Eupelops acromios	12	8.0	6.3
Dolicheremaeus elongatus	3	9.0	5.7
Truncopes sp.	4	11.6	6.4
Fissicepheus clavatus	158	12.9	4.7
Liacarus gammatus	3	13.0	5.1
Oppia sp.1	8	14.4	6.6
Liochthonius sellnicki	23	14.7	3.4
Hermanniella sp.	4	15.4	4.1
Camisia spinifer	14	16.7	7.0
Cultroribula lata	78	16.7	3.5
Suctobelba sp. 9	32	17.3	2.8
Brachychthonius elsosneadensis	54	17.7	5.4
Tectocepheus velatus	491	17.9	5.8
Multioppia brevipctinata	3	18.1	2.5
Tectocepheus cuspidentatus	135	18.3	4.5
Paraeacaroides pacificus	27	18.7	5.7
Suctobelba sp.6	47	18.8	2.7
Suctobelbella frondosa	26	18.8	1.4
Suctobelba sp. 3	26	18.9	3.3
Suctobelba sp.8	25	19.2	4.0
Suctobelba sp.5	16	20.0	2.7
Suctobelba sp.4	17	20.2	4.7
Liochthonius intermedius	133	20.5	5.8
Brachychthonius sp.	23	23.6	5.2
Ceratoppia quadridentata	61	23.6	11.2
Neoribates roubali	3	24.0	7.2
Goyoppia sagami	224	24.5	6.2
Oribatula sakamorii	9	24.7	5.6
Hoplophthiracarus pavidus	247	24.8	7.4
Rhysotritia arudua	7	25.9	4.3
Epidamaeus fragilis	28	26.4	6.1
Suctobelba sp.1	229	27.0	7.4
Suctobelba sp.2	185	27.4	8.2
Trimalaconothrus sp.	7	27.4	12.9
Eremobelba japonica	5	27.6	9.0
Platynothrus peltifer	4	27.8	9.7
Xylobates sp.	6	28.8	10.9
Hermannia kanoi	72	29.0	10.0
Mesotritia okuyamai	3	29.4	8.2
Carabodes rimosus	9	30.4	10.1
Oppiella nova	233	30.5	7.6
Nothrus biciliatus	3	31.0	10.9
Epilohmannoides esulcatus	10	31.7	10.7
Defectamerus crassisetiger	5	32.3	11.9
Rostrozetes ovulum	26	32.7	8.4
Brachychthonius hungaricus	80	34.6	7.2
Sellnickochthonius zelawaiensis	13	36.4	10.1
Quadroppia quadricarinata	11	40.1	8.2
Malaconothrus sp.3	23	41.5	6.8

The succession index of species ranged from 4.4 to 35.1 months in Collembola, from 8 to 41.5 months in Cryptostigmata. The frequency distributions for the succession index of species are shown in Fig. 4. 7. The proportion of Collembolan species showing succession indices less than 12 months was 35%, while that for Cryptostigmata species was only 8%. In contrast, the proportion of Collembolan species showing more than 24 months was 20%, while that for Cryptostigmata was about 50%.

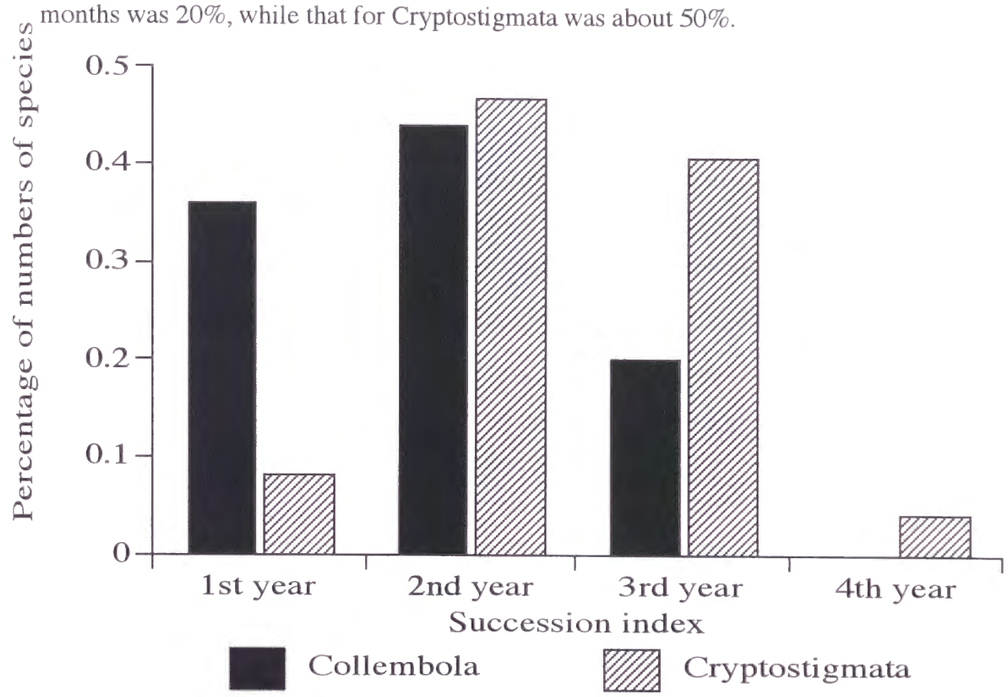


Fig. 4. 7. Frequency distribution of the succession index of species of the Collembola and Cryptostigmata communities

Fig. 4. 8 shows the succession index for each colonizing group. Here the population data of composing species were summed for each group, and the succession index for each group was calculated. In the Cryptostigmata community, a typical early colonizing group as in the collembolan community was not recognized. The centre of gravity of Cry 1 was located between Col 1 and Col 2, and that of Cry 2 was located between Col 2 and Col 3.

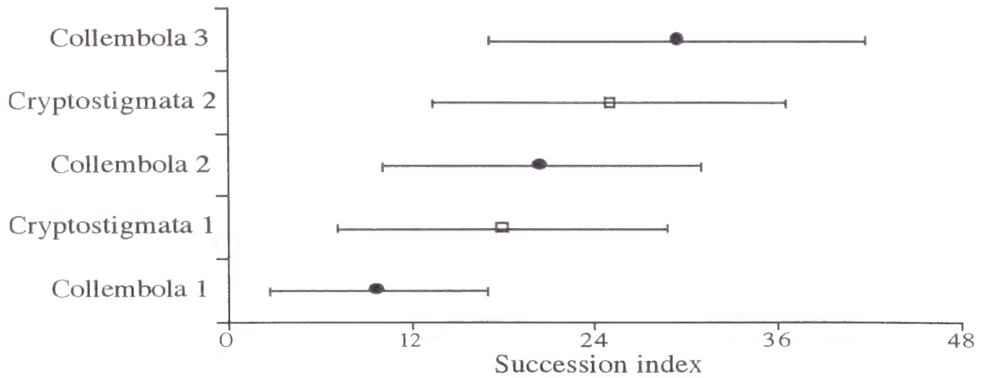


Fig. 4. 8. Succession index for Collembola and Cryptostigmata colonization groups. Bars indicate the standard deviations

Similarity index of collembolan and Cryptostigmata communities

Similarity of the species composition of the collembolan and Cryptostigmata communities between years was examined using the index of Pianka's α. In this comparison the samples in the February (i.e., 12, 24, 36, 48 months) were used to exclude the influence of seasonal differences in the community. In the Collembola community the similarities were high (more than 0.8) and constant in all comparisons (Fig. 4. 9). In contrast, in the Cryptostigmata community the similarities decreased with the time difference in the comparison. It shows that the collembolan community was similar over a 4 year period, whereas the composition of Cryptostigmata community continued to change throughout the 4 year period.

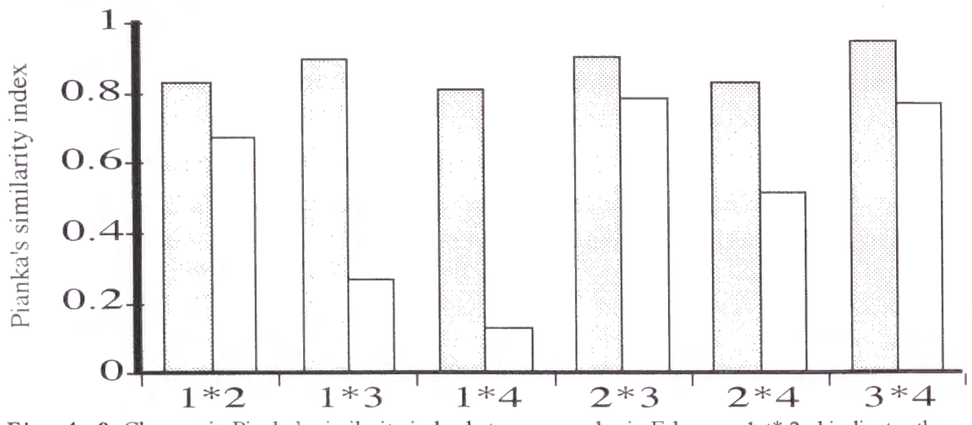


Fig. 4. 9. Changes in Pianka's similarity index between samples in February. 1st* 2nd indicates the value between the sample in 1st year's February and that in 2nd year's February

Niche Breadths and Niche overlap for the main Collembola and Cryptostigmata species

The niche breadths (RB) and niche overlaps (α_{hi})of the main collembolan and Cryptostigmata species mentioned before (11 species for Collembola and Cryptostigmata) are shown in Table 4. 3. The average niche breadths of the total main species are almost the same (0.69-0.72) between Collembola and Cryptostigmata. The value of Col 2 group was higher than those of other groups.

The niche overlaps (α_{hi}) are shown as the average values for combinations of two different species among Collembola and Cryptostigmata. The total numbers of pairs were 55 for Collembola and Cryptostigmata. The values of groups were averages of combinations of species within each group. The average values of α_{hi} for total combinations are higher in Cryptostigmata (0.53) than in Collembola (0.41). The values for each group were also higher in Cryptostigmata (0.71-0.76) than in Collembola (0.46-0.68).

Table 4. 3. Average niche breadths and niche overlaps for main Collembola and Cryptostigmata species in each cluster group

Values are shown in averages ± standard deviations.

Niche overlaps values were calculated for the combination of species in each cluster group

		Group			Total
		1	2	3	
Collembola	Niche breadths	0.66±0.17	0.82±0.08	0.61	0.69±0.15
	Niche overlaps	0.59±0.27	0.68±0.19	0.46	0.41±0.25
Cryptostigmata	Niche breadths	0.68±0.09	0.74±0.09	-	0.72±0.09
	Niche overlaps	0.71±0.11	0.76±0.13	-	0.53±0.26

Discussion

Changes in soil animal abundances

In Mor and Moder humus forms, Collembola and Acari are major decomposers (Petersen & Luxton 1982). In this study, the litter bag fauna mainly consisted of Collembola and Acari. Faunal abundances per gram of litter increased with the phase of decomposition, which suggests that the litter bags provided favorable physical and food conditions for the colonization of soil animals. Other studies have also reported an increase in faunal abundance with the advance of decomposition (Hågvar & Kjøndal 1981; Seastedt and Crossley 1983; Takeda 1988,1995)

The importance of litter moisture has been often shown for the colonization of Collembola and Cryptostigmata (Verhoef & Witteveen 1980; Vegter 1983; Joose & Veltkamp 1970; Lebrun 1969). In this study low moisture content in the litter likely inhibited colonization by microarthropods, resulting the low density levels in the first year. Density of soil animals in a litter bag increased in the second year and remained fairly constant over the study period. Litter falls in the winter covered the litter bags and thus, environmental extremes in temperature and moisture are ameliorated for the colonization of soil animals.

Community organization of Collembola and Cryptostigmata during decomposition process

In this study, Cryptostigmata and Collembola were predominant groups and occupied similar abundances in the litter bag fauna. But the species richness of communities was higher in the Cryptostigmata community than in the Collembola. Furthermore, the Cryptostigmata community consisted of more species with relatively similar abundances, while the Collembola community was dominated by fewer than ten species (Fig. 4.2). The difference between Cryptostigmata and Collembola community structure can be related to the differences in the colonizing patterns of composing species during the decomposition. Thus, the colonizing patterns of Collembola and Cryptostigmata species were quantified by the diversity index, succession index, similarity index and niche analysis.

The Collembola as a whole were earlier colonizers than Cryptostigmata during the

decomposition in this study. Bolger (1985) and Takeda (1988) also suggested that Cryptostigmata mites were late colonizers in the decomposition phases. In the diversity changes, Cryptostigmata and Collembola communities showed similar seasonal trends during the first year, but the Cryptostigmata community increased its diversity after 12 months (Fig.4.3).

The frequency distributions for the succession index about species numbers are shown in Fig. 4.7. The modes of the succession index values were different between the two taxa. Collembola were early colonizers and had a mode at about 1.5 years. The Cryptostigmata community had a mode of the succession index values at 2.5 years. The similarity of the Cryptostigmata community between years decreased with the time difference, while the similarity of Collembolan community between years was not so different (Fig. 4.9). These results suggest that the most collembolan species had completed their colonization within the first year, and then collembolan species composition did not change after the second year. In contrast, the species composition of Cryptostigmata changed gradually even after the second year. Thus, the Cryptostigmata species were later colonizers than collembolan species.

The colonization patterns of species were quantified by the niche utilization pattern of each species along the colonizing time gradient. The niche utilization patterns of species were shown by the combination of niche breadths and niche overlap of populations within the community. In this litter bag study, total colonizing time was 48 months, and the niche breadths were not so different between the main species of Collembola and Cryptostigmata groups (Table 4.3). But the niche overlap values of the main species were higher in Cryptostigmata than in Collembolan communities. It means that the average niche breadths in terms of colonization time were similar between Collembola and Cryptostigmata, but the species packing was higher in the main species of Cryptostigmata on the gradient of colonization time.

5. The interactive process of microorganisms and soil animals in the decomposition of pine needles

Study of feeding attributes of soil animals is important for an understanding of their role during the decomposition. Collembola and Cryptostigmata are detritivorous or fungivorous in their feeding habits (Luxton 1972; Petersen & Luxton 1982), and exploit food resources such as fungi and plant debris provided during decomposition processes of litter. Studies of feeding habits of Collembola (Anderson & Healey 1972; Whittaker 1977; Addison & Parkinson 1978; Visser and Whittaker 1981) and Cryptostigmata (Luxton 1972; Behan & Hill 1978; Behan-Pelletier & Hill 1983; Wallwork 1983; Kaneko 1988) shows that they are detritivorous or fungivorous, and exploit food resources such as fungi and plant debris. Therefore the function of these two taxa in decomposition processes has been categorized in saprotrophic invertebrates (Swift et al. 1979).

Takeda & Ichimura (1983) generalized that in laboratory studies most collembolan species show a clear preference among available foods. In contrast, field populations usually show no food preferences as indicated by the examination of gut contents of animals collected in the field which consisted largely of the most abundant foods in soil such as decomposing plant matter and fungi. Anderson (1977) suggested that variations in feeding habits of Cryptostigmata are relatively small in comparison with higher specialization in microhabitat use. Kaneko (1988) showed the specialization of feeding habits and mouthparts for Cryptostigmata, and proposed four feeding habits for Cryptostigmata species. And he suggested that the variation in feeding habits of Cryptostigmata should partially contribute to increase species diversity by means of specialization on food resource use as well as microhabitat use. Cryptostigmata may specialized feeding habits more than Collembola. But most of studies for feeding habits have not been related with the resource condition during the decomposition processes of litter. Collembola may finely specialize their feeding with the resource condition during the decomposition processes of litter. Joint studies of soil animal populations and resource dynamics of decomposing litter are important for the interpretation of successional patterns of soil animals, since these changes are responses of species to the availability of food resources during decomposition processes. The precise analysis of feeding habits related with the decomposition processes especially for Collembola are needed.

In this chapter the successional pattern of Collembola and Cryptostigmata were related with the fungal colonization and nutrient dynamics mentioned in Chapter 3 and 4.

The successional changes of Collembola and Cryptostigmata are explained through the analysis of their feeding attributes during the decomposition processes of pine needle litter in a pine forest. Especially feeding habits of Collembola are investigated precisely related with resource conditions during decomposition. A further aim of this chapter is to asses the roles of Collembola and Cryptostigmata species in decomposition species. In the latter part of this chapter, the interactive processes of microorganisms and soil animals during decomposition of pine needle litter are discussed.

Material and methods

Gut content analysis

In this study plot, soil fauna was dominated by microarthropods such as Collembola and Acari. The life cycles and population dynamics of collembolan species have been studied at this site by (Takeda 1976, 1979, 1984, 1987). In this plot, the collembolan community consists of 36 species and collembolan species were divided into two feeding groups, i.e. 5 suctorial and 31 detritivore species, on the basis of mouth-part morphology. The detritivore species were dominant in the collembolan community in terms of population abundance and species numbers (Takeda & Ichimura 1983). In this study, four detritivorous species were selected for the gut content analysis. Two species, *Folsomia octoculata* and *Onychiurus flavescens*, were humus-dwelling species. The other two species, *Tomocerus varius* and *Lepidocyrtus lignorum* , were surface-dwelling species (Takeda 1979). In this study, the feeding habits of main species except of four collembolan species were investigated through the rough observation by microscope. In the observation, a cover-glass was placed on a specimen and was squashed with finger pressure.

The specimens of the four species were sorted from samples and preserved in lactic acid for one week. For each species, the number of individuals with gut contents was counted. The specimens with visible gut contents could then be selected for further analysis. On each sampling occasion, thirty fed individuals were selected from each species. They were divided into three sub-samples containing 10 individuals and their gut contents were combined for analysis. The gut contents of 10 individuals were mounted in a small drop of glycerol on a glass slide and dispersed by lightly pressing the cover slip.

Seven categories of foods were classified as follows; plant tissues, amorphous mass, fungal hyphae, fungal spores, pollen, mineral particles, and animal remains. Gut contents were examined with a binocular microscope of 400 X magnification. The area of each food particle was measured by a microscope with a gridded eyepiece having a total of 100 squares. Five replicates of (i.e. 500 squares) views were examined for each gut sample. The percentage of each food was calculated on the basis of their relative areas.

Results

Genaral feeding habits of main species of Collembola and Cryptostigmata

Table 5.1 General feeding habits of main Collembola and Cryptostigmata species.

	Species	Feeding habits
Collembola	*Lepidocyetus lignorum*	micro.
	Homidia subcingula	micro.
	Tomocerus varius	micro. / pan.
	Isotoma sensibilis	micro.
	Onychiurus flavescens	pan.
	Folsomia octoculata	pan.
	Tullbergia yosii	pan. / frag.
	Tetracanthella sylvatica	pan.
	Odontera sp.	invisible
	Xenylla humicola	pan.
	Meganthorax minimus	pan. / frag.
Cryptostigmata	*Suctobelba sp.1*	frag.
	Hoplophthiracarus pavidus	macro.
	Oppiella nova	micro.
	Hermannilella kanoi	pan.
	Suctobelba sp.2	micro.
	Brachycochthonius hungaricus	micro.
	Goyoppia sagami	micro.
	Fissicepheus clavatus	pan.
	Ceratoppia quadridentata	micro.
	Brachycochthonius elsosneadensis	micro.
	Tectocepheus velatus	pan. / frag.

macro.= macrophytophages; micro. = microphytophages; pan. = panphytophages; frag.= fragment feeders.

Table 5.1 shows the feeding habits of main species of Collembola and Cryptostigmata species. In this table the nomenclatures for feeding habits were obeyed by Kaneko (1988). He categorized four types of feeding habits: 1) Macrophytophage- feeding on higher plant matter, 2) Microphytophage - feeding on fungal hyphae and spores, 3) Panphytophage - feeding on higher plant matter and fungal material, 4) Fragment feeder - feeding on finely fragmented higher plant matter and fungi.

In *Odontera* sp., they have no visible gut contents. They may be suctorial feeders. In *Ceratoppia quadridentata*, some individuals have animal remains (perhaps collembola body) in their gut contents.

Changes in gut contents of selected Collembola species

In every species, gut contents consisted largely of plant and fungal materials and the other components constituted a minor proportion of their food (Table 5. 2).

Table 5. 2. Mean composition of the gut contents of Collembola during the experimental period

	Tomocerus varius	*Folsomia octoculata*	*Onychiurus flavescens*	*Lepidocyrtus lignorum*
Plant material	64.5	76.7	81.9	47.2
Fungal hyphae	34.3	22.8	17.7	44.2
Fungal spores	0.5	0.3	0.2	8.5
Pollen	0.3	0.1	0.0	0.0
Mineral particles	0.2	0.1	0.1	0.1
Algae	0.1	0.0	0.1	0.0
Animal remains	0.1	0.0	0.0	0.0

Fig. 5. 1 shows the variations in percentages of plant and fungal material in gut contents of the four species over a 2 year period. For each species, the variations of plant

and fungal material during the decomposition process were examined using ANOVA. The proportion of plant and fungal materials in the guts of *T. varius* and *F. octoculata* showed a significant variation in gut contents over the study period ($P < 0.01$). Changes in feeding preferences of *T. varius* and *F. octoculata* were examined by the regression analysis between the decomposition time (month) and percentages of fungal materials in each species. The results are shown in Fig. 5. 2. At the first sampling, the proportion of fungal materials in the gut contents of *T. varius* and *F. octoculata* were 45 and 30% respectively. Then the percentage of fungal material in gut contents of the two species decreased with the advance of decomposition stages. The two species showed a switch in their feeding from fungal to plant material as the decomposition advanced. Switching of feeding from fungal to detritus materials was more pronounced in *T. varius* than in *F. octoculata*.

In the cases of *L. lignorum* and *O. flavescens*, there was no switching of feeding during the decomposition process. The overall mean proportions of fungal materials in the gut contents of *L. lignorum* and *O. flavescens* were 55 and 20% respectively and those of plant materials were 45 and 80% respectively. There were significant differences in the gut contents between the two species over the study period in that *L. lignorum* and *O. flavescens* specialized in fungal and detritus feeding respectively.

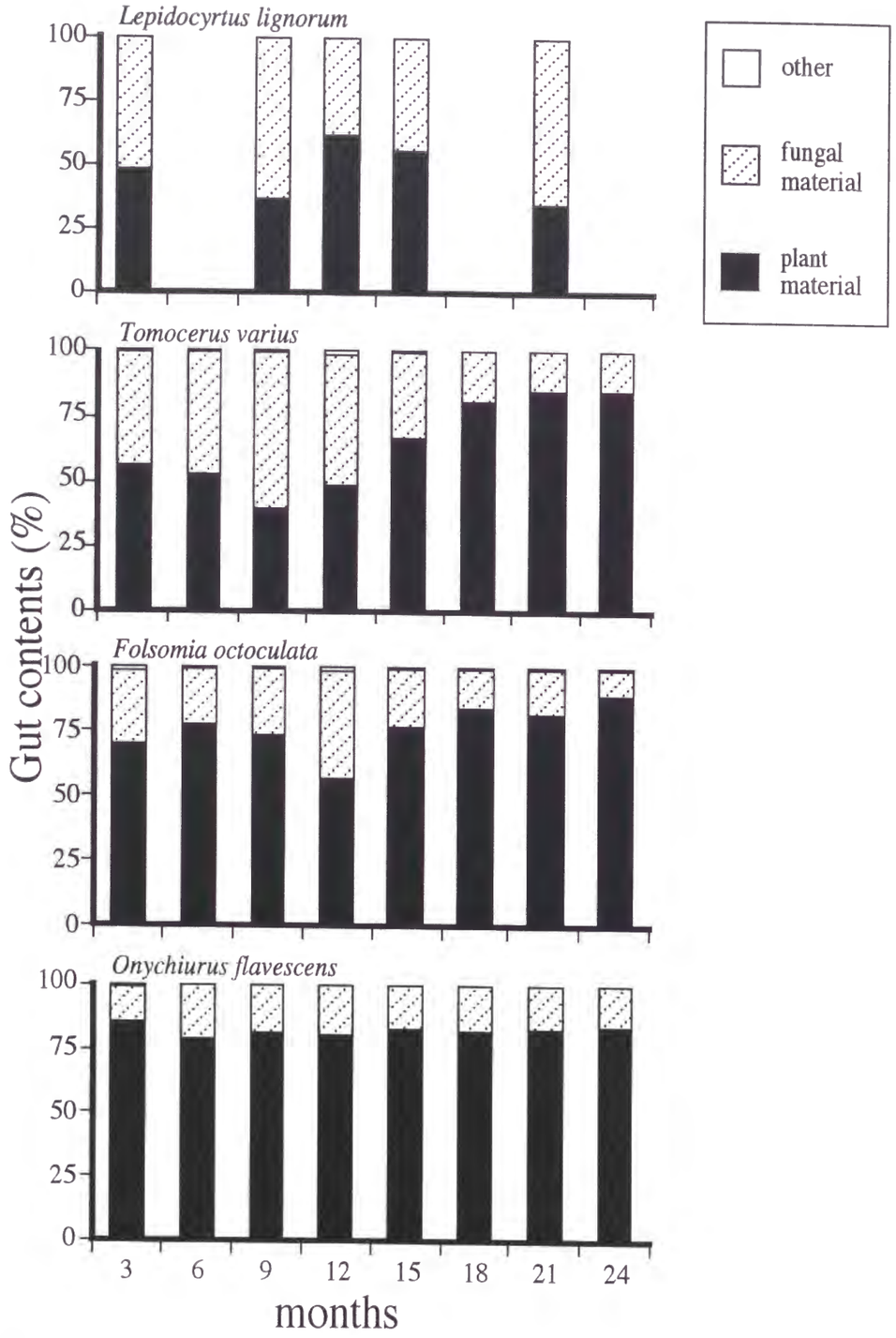


Fig. 5. 1. Gut contents of four species of Collembola.

Correlation between abundances of soil arthropods and carbon to nutrient ratios

The carbon to nutrient ratios represent the resource quality of litter for the soil animals. So, the correlation coefficients between densities of soil arthropods and carbon / nutrient ratios were examined. There were significant relationships between total soil arthropod densities and C/N and C/P ratio (for C/N, $p < 0.01$, $r = -0.772$, d.f. = 8; for C/P, $p < 0.05$, $r = -0.767$, d.f. = 8). Among the soil animal groups, Cryptostigmata showed significant correlations between the densities and C/N and C/P ratios (for C/N, $p < 0.05$, $r = -0.832$, d.f.= 8; for C/P, $p < 0.01$, $r = -0.771$, d.f. = 8). There were negative correlations between densities of other soil animal groups and C/N and C/P ratios, except for Prostigmata, but the correlation coefficients were not significant at the level of $p < 0.05$.

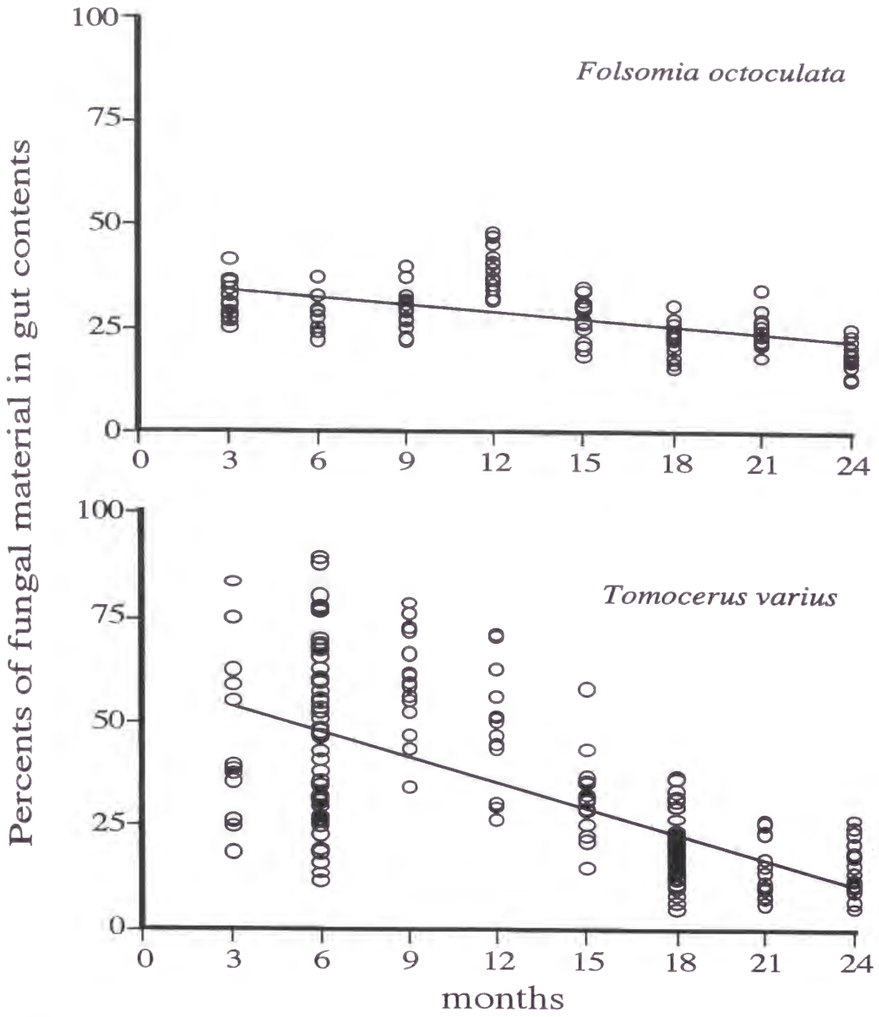


Fig. 5. 2. Changes in percentage of fungal material in gut contents. Dots show the values for each sample. The formula of a solid lines are Y= -0.538X + 35.9. R2 = 0.285 (*F. octoculata*) and Y= -2.06X + 60.2, R2 = 0.444 (*T. varius*) where X = months after the experiment has started, Y = percentage of fungal material in gut contents.

Correlation of main species of Collembola and Cryptostigmata with the changes in C/N ratio of the needles

Correlation coefficients of density of the main species of Collembola and Cryptostigmata with the changes in C/N ratio of the needle litter are shown in Table 4. 4. The collembolan species may be classified into three categories (i.e. positive, negative and no correlation) according to the relation with the C/N ratio.

Two species in Col 1 have significant positive correlation with the C/N ratio (*Lepidocyrtus lignorum* and *Homidia subcingula*). *Tomocerus varius* and *Isotoma sensibilis* also showed positive correlation. In the Col 2 group *Onychiurus flavescens* has a significant negative correlation with the C/N ratio. In Col 2 and Col 3 *Folsomia octoculata, Tetracanthella sylvatica* and *Tullbergia yosii* also showed negative correlation. *Odontella* sp.and *Xenylla humicola* had very low correlation coefficients with C/N.

In the Cryptostigmata community, Cry 1 species have very low correlation coefficients with C/N. In Cry 2 *Oppiella nova, Hermannia kanoi*, *Hoplophthiracarus pavidus* and *Suctobelba* sp.1 have significant negative correlation with C/N. *Goyoppia sagami, Brachychthonius hungaricus* and *Suctobelba* sp.2 also showed negative correlation.

Table 5. 3. Correlation coefficients for linear relations between C/N ratios of litter and densities (per gram of litter) of main species in the Collembola and Cryptostigmata communities

	Species	Groups in cluster analysis	Coefficients of correlation
Collembola	*Lepidocyrtus lignorum*	1	0.746*
	Homidia subcingula	1	0.681*
	Tomocerus varius	1	0.568
	Isotoma sensibilis	1	0.417
	Onychiurus flavescens	2	-0.668
	Folsomia octoculata	2	-0.630
	Tullbergia yosii	3	-0.463
	Tetracanthella sylvatica	2	-0.417
	Odontera sp.	1	0.097
	Xenylla humicola	1	0.253
	Megalothorax minimus	3	0.330
Cryptostigmata	*Suctobelba* sp.1	2	-0.736*
	Hoplophthiracarus pavidus	2	-0.692*
	Oppiella nova	2	-0.671*
	Hermannia kanoi	2	-0.638*
	Suctobelba sp.2	2	-0.593
	Brachychthonius hungaricus	2	-0.549
	Goyoppia sagami	2	-0.524
	Fissicepheus clavatus	1	-0.016
	Ceratoppia quadridentata	1	-0.044
	Brachychthonius elsosneadensis	1	-0.156
	Tectocepheus velatus	1	-0.258

*; $p<0.05$

Discussion

The relation of feeding habits and community organization during decomposition

In the Chapter 4, I showed that colonization pattern were different between Collembola and Cryptostigmata communities. The difference of the colonization patterns between species might indicate the different response of the species to the change of resource quality of decomposing litter. Correlations of the densities of Collembola and Cryptostigmata species with the C/N ratios of decomposing litter were analyzed (Table 5. 3). Dominant species in the Col 1 group showed positive correlation with the C/N ratios and are early colonizers, while dominant species of Col 2 and Col 3 showed negative correlation with the C/N ratios and can be grouped into the late colonizers. In the Cryptostigmata community no dominant species have positive correlation with the C/N ratios, dominant species in Cry 1 and Cry 2 are negatively correlated with the C/N ratios and can be recognized as late colonizers. Thus, the main collembolan species showed different responses to the C/N ratios between the two colonization groups, while the nine main species of Cryptostigmata showed similar responses to the C/N ratios.

These different responses to C/N ratios between Collembola and Cryptostigmata species can be related to their feeding attributes. The decomposition processes of pine needles were characterized by the litter quality and by the fungal and animal abundances (Table 5. 4). In this study, the fungal colonization patterns were characterized by the three stages as follows: 1). growth stage during 3 to 9 months, 2). steady-state stage during 12-18 months, and 3).collapse stage during 21 to 48 months. The contributions of fungi to nitrogen and carbon dynamics have also been shown in a number of decomposition studies of leaf litter (Berg & Söderström 1979; Bååth & Söderström 1979; Ausmus et al. 1979). During the decomposition process, such changes in litter quality are brought about by fungal growth which thus facilitates the colonization of Collembola.

The changes in abundances of the four collembolan species and the gut contents of the Collembola were studied in conjunction with food availability during the decomposition phases. In the nutrient immobilization phase, fungal populations grew and *T. varius*, and *L. lignorum* were predominant. Analysis showed that *T. varius* and *L. lignorum* had higher proportions of fungal materials in their guts during this phase, suggesting that the two species grazed selectively on fungal material. Hågvar & Kjøndal (1981) showed that *L. lignorum* was a typical microphytophage, and was a pioneer species in the early decomposition stages of birch litter. The pioneer species have the

strategy of a high mobility in the litter layer and a well-developed ability to identify their food items, such as fast-growing, spore-producing fungal colonies, in their microhabitat.

With decomposition proceeding, the C/N ratio became low and humus and animal feces increased in the steady state phase. In this phase, the abundances of *F. octoculata and O. flavescens* increased with the decomposition process and were significantly negatively related to the C/ N ratio of needle litter. *O. flavescens and F. octoculata* continued to increase even after 24 months during the mobilization phase of needle litter (Takeda 1987). The two species had low proportions of fungal materials and the gut contents consisted of high proportions of plant material. The detritivorous Collembola can consume plant detritus partially digested by microbial populations. In this study the two fungivorous collembolan species were early colonizers, while the two detritivorous species were later colonizers in the decomposition. These changes in abundance were related to the feeding attributes of the species. Thus, the successional changes of the four collembolan species were explained by their feeding habits and were related to food availability in each decomposition phase.

The feeding habits of soil animals are many and varied (Petersen & Luxton 1982). However, here the joint study of collembolan populations and food resources revealed two feeding strategies, i.e. specialist and generalist feeding. *O. flavescens and L. lignorum* were specialists in their feeding habit, the former being fungal feeding, the latter plant debris feeding. The early colonizer, *L. lignorum*, was fungivorous and the pioneer species in the decomposition stages. The pioneer species are less abundant compared with species inhabiting the thick underlying organic layers because the microbial "flush" period is short and normally limited to a thin top litter layer. The other specialist, *O. flavescens,* depends upon the decomposing plant litter and its population density was high in the moder humus forms (Takeda 1987). *T. varius and F. octoculata* were generalists in their feeding habits, selecting food according to its availability in each of the decomposition stages. The proportions of fungal material in their guts decreased during litter decomposition when they switched from fungivore to detritivorous to detritivorous.

Such a switching of feeding habit was shown for some Cryptostigmata (Acari) species during the decomposition of leaf litter by Anderson (1975) and was attributed to increased palatability of plant materials after leaching of poly-phenols from leaf litter during decomposition. The ability of switch to their feeding habits allows collembolan species to exploit wider food niches. In this study area, *T. varius* and *F. octoculata* are each dominant surface and humus dwelling species respectively (Takeda 1979, 1987). The dominance of the two species may be explained by the switching ability in their

feeding depending upon the availability of food items during the decomposition states in the organic soil layers. The generalist feeding of Collembola may also provide an explanation for the differences of feeding selection of collembolan species noted between the field and laboratory studies (Takeda & Ichimura 1983).

The successional changes in the collembolan species may be explained by the feeding attributes of species in response to the resource availability at each decomposition phase. In contrast, successional changes of Cryptostigmata species were not simply explained by the feeding attributes of species. In the present study, the feeding habits of Cryptostigmata were not quantitatively investigated. Table 4. 1 shows that the main species of the Cryptostigmata community have variable feeding habits particularly in the species occurring in the late decomposition phase. For example, Oppiidae species (Oppiella nova and Goyoppia sagami) are microphytovorous in the observation and known as a fungal feeders (Hartenstein 1962; Luxton 1972; Kaneko 1988). Phthiracaridae (Hoplophthiracarus pavidus) are macrophytovorous in the observation and some studies (Hayes 1963; Luxton 1972; Anderson 1975) suggested that they feed mainly upon mesophyll cells and deposit faeces in the feeding cavity within needles. In addition, in the gut of Suctobelbidae species fragmented materials were found to dominate in the microscopic observation. So the later colonizing species of Cryptostigmata showed three different feeding habits; fungal-, macrophyto- and fine particle feeding. This separation of species along the dimension of food resources might complement the high overlap values on the colonizing time gradient (Schoener 1974) and facilitate the coexistence of species within the Cryptostigmata community which are more numerous than those of collembolan community.

In conclusion, the feeding attributes of collembolan species changed from fungal grazers to detritivores in response to the change of resource quality. Collembola colonized earlier than Cryptostigmata due to the presence of early colonizing fungal grazers in high abundance. Cryptostigmata utilized a wider range of the decomposition phase as a whole community and continued to change community structure even in the late decomposition phase. Cryptostigmata in the late decomposition phase might have variable feeding habits among the main species (Wallwork 1983), and utilize other more dimensions of niche such as specialization of microhabitat and food items (e.g. mesophile in the needle) (Luxton 1972). The wide utilization of resource gradients, together with the varied feeding habits of Cryptostigmata, might enable the coexistence of more species in their community than is the case with Collembola.

Table 5. 4. Relation of main Collembola and Cryptostigmata species densities with characters of two decomposition phases, i.e. the early phase from 3 to 18 month and the late phase from 21 to 48 months, in terms of nitrogen states, C/N ratio and fungal abundances

Decomposition phase	early phase		late phase
Time (months)	3 - 9	12 - 18	21 - 48
Fungal condition	growth stage	steady-state stage	collapse stage
Nitrogen	leaching	steady-state	steady-state
C /N ratio	75.9 - 155	56 - 75.8	35.9 - 53.7
Correlation with C/N	**Positive**		**Negative**
Collmbola	*Lepidocyrtus lignorum*		*Onychiurus flavescens*
	Homidia subcingula		
	(weak correlation)		(weak correlation)
	Tomocerus varius		*Folsomia octoculata*
	Isotoma sensibilis		*Tullbergia yosii*
			Tetracanthella sylvatica
Cryptostigmata			*Suctobelba* sp.1
			Hoplophthicarus pavidus
			Oppiella nova
			Hermannia kanoi
			(weak correlation)
			Suctobelba sp.2
			Brachychthonius hungaricus
			Goyoppia sagami
	Non successional		
Collembola	*Xenylla humicola*		
	Odontella sp.		
	Megalothorax minimus		
Cryptostigmata	*Tectocepheus velatus*		
	Fissicepheus clavatus		
	Ceratoppia quadridentata		
	Brachychthonius elsosneadensis		

In this study, faunal abundances were not correlated with the decomposition rates during the decomposition processes. Takeda (1988) suggested three explanations for the decrease in decomposition rates with increasing decomposer abundances as follows; (1) indirect effect of soil animals to decomposition, (2) recycling of organic matter and (3) methodological problems of litter bags.

Fig. 5. 3 shows the schematic model for decomposition process of pine needles. In the immobilization phase, the soil animals may control the microbial metabolism through their grazing activities. The surface-dwelling Collembola species, *T. varius* and *L. lignorum* utilize the fungi colonizing the needle surfaces in the immobilization phase, during which fungal populations were in a growth phase. The surface-dwelling Collembola species may be contributing to the immobilization process of fungi by eliminating the senescent hyphae through their grazing activities. Such effects have been demonstrated for Collembola in the laboratory (Hanlon & Anderson 1979; Ineson et al. 1982; Setälä et al. 1991). The surface-dwelling species predominated in the L layer but their population may be variable depending upon environmental conditions such as humidity. The grazing Collembola may also be prevented from over-exploiting fungal populations by limitations imposed by predation pressures and environmental variability in the L layer. Thus, they might promote nitrogen immobilization rather than mobilization by fungal populations through their gazing activities. During the immobilization of fungal populations, the needle litter was changed into fungal biomass (alive and senescent) and the grazing Collembola deposited their feces on the needle surfaces. The interaction between the grazing Collembola and fungal populations may increase food availability for the detritivorous collembolan species. In the later decomposition stages, the decomposition rates decreased, while the collembolan abundances usually increased (Takeda 1994, 1987).

After the collapse stage of fungal community, the needles entered into the late decomposition phase (table 5. 4). The late decomposition phase might be controlled by the utilization of refractory components such as lignin material by microbial and animal populations (Berg 1986). Lignin degrading fungi need another C source to decompose lignin (Kirk et al. 1976). Thus, in the late decomposition phase, the microbial activities may be limited by the carbon sources. So, the carbon sources for the microbial decomposition may be supplied from the cellulose exposed by the comminution of soil

animals. Anderson & Healey (1973) suggested that coprophagy might be expected to be a major industry among soil animals. Coprophagy is a sort of recycling utilization of resources and may increase food availability for the detritus feeder. The later colonizing species, *O. flavescens* and *F. octoculata*, may contribute to the recycling of organic matter through their coprophagy and detritus feeding. Decomposition processes of pine needles consisted of immobilization and mobilization phases. The specialist feeders contributed to either the grazing effects in the immobilization phase or the recycling process in the mobilization phase, while the generalist feeders contributed to both processes and were dominant in the Moder humus form in this study area.

Table 5. 4 shows the increase of Cryptostigmata abundance in the late decomposition phase. A species of Phthiracarid mites (*Hoplophthiracarus pavidus*) increased in the late decomposition phase of this study. These mites feed mainly upon mesophyll cells and deposit faeces in the feeding cavity within needles. Takeda (1995) showed that the number of feacal pellets of Cryptostigmata and needles attacked by Cryptostigmata increased exponentially with the advance of decomposition. In the late decomposition phase, detritus feeding Collembola increased their abundances (Hasegawa & Takeda 1995). These feeding of Cryptostigmata and Collembola may increase the exposed site of organic matter for microorganisms. The detritus and endophageous feeder might be important for the carbon and nutrient mobilization of coniferous litter in the late decomposition phase. The detritus feeding might contribute to the recycling of organic matter such as animal faeces and decomposition products.

The Moder humus form is characterized by the microarthropod faecal aggregates in the F layer (Bal 1970; Green et al. 1993). Thus, carbon and nutrients of litter slowly mobilized through the recycling of organic matter in the F layer. The grazing effect of the animals might occur mainly in the early decomposition phase, when the microbial activity is high. While, the comminution effect may be important in the late decomposition phase. The grazing effects of Collembola and Cryptostigmata on the immobilization phase of litter have been emphasized in literatures (Verhoef & Brussard 1990). While, the effects of soil arthropods to the late decomposition phase are still unclear. More detailed studies of the late decomposition phase and the roles of micro-organisms and soil animals are needed to know the carbon and nutrient dynamics in the recycling systems of the soils.

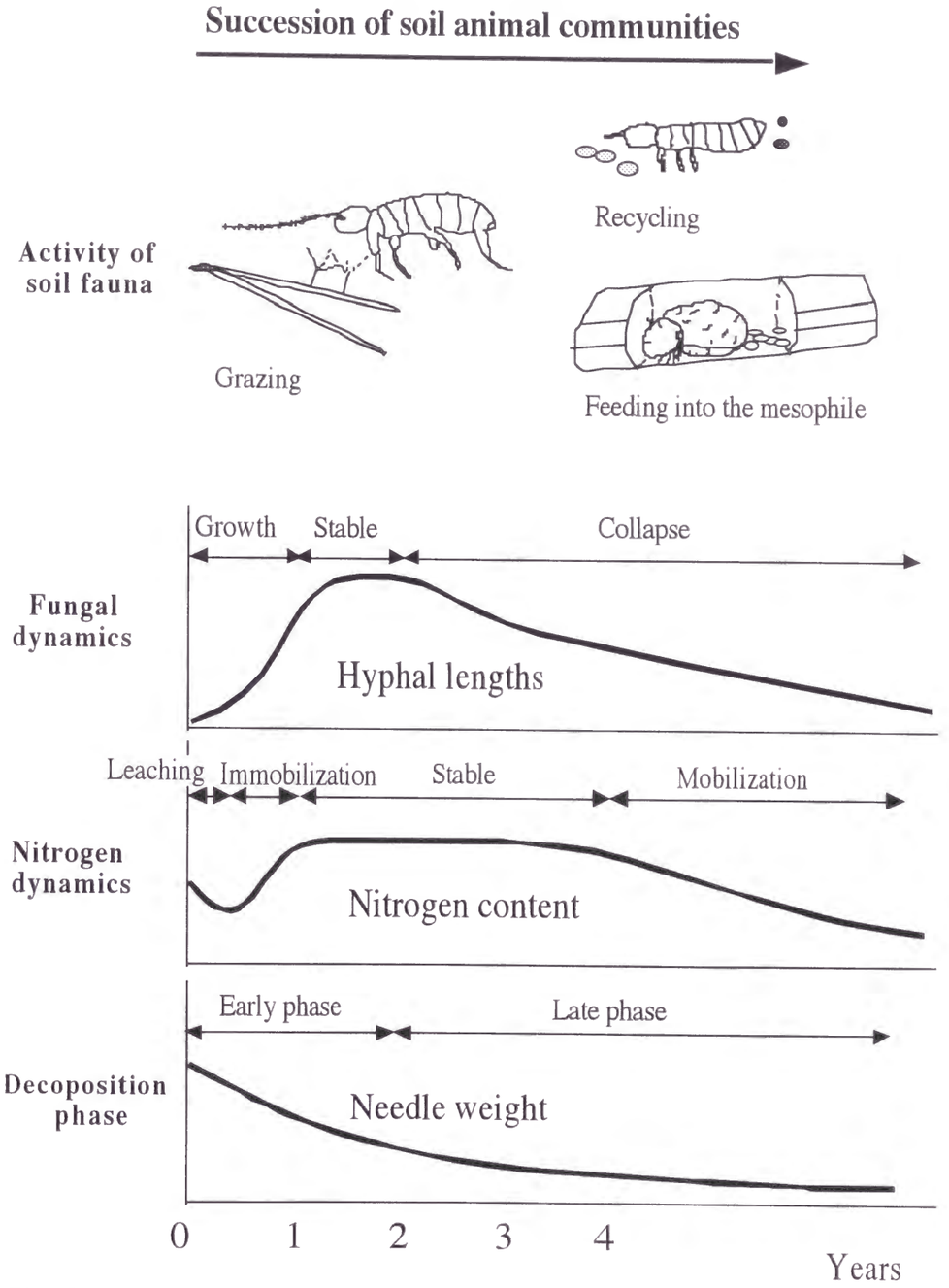


Fig. 5. 3. The shematic model of the role of fauna during the decompostion process of pine needles

6. Summary

Decomposition of leaf litter has been demonstrated the weight and chemical changes during the decomposition process. But there were rather few studies showing the interactions between litter quality, fauna and microbial populations during decomposition. And such studies followed over only one or two years period, so the roles of soil microorganisms and soil animals in the late decomposition phase are still obscure. The objectives of this research study are to show the pattern of pine needle decomposition in terms of nutrient dynamics (C, N, P, K, Mg, Ca) and fungal and soil animal population dynamics over a four year period in a coniferous forest soil with a moder humus form, and to interpret the successional changes of Collembola and Cryptostigmata during the decomposition processes of pine needle litter. A further aim of this thesis is to assess the role of soil fungi and arthropods in the decomposition phases of *Pinus densiflora* litter.

1. From the review of decomposition process and the ecology of soil animals, it was suggested that the decomposition of pine needle litter should be investigated from the joint study of substrates, microorganisms and soil animals.

2. The study site was red pine forest and the humus form is a Moder with a poorly developed mineral soil horizon (A) which is about 1cm in thickness. The A_0 layer consists of L, F, and H layers, ranging fro 2 to 5cm in thickness.

3. It was concluded that two decomposition phases (i. e. early and late phase) produced the different colonizing conditions for the soil animals. In the early decomposition phase fungal conditions were in growth stage or in steady state, while in late decomposition phase fungal conditions were in collapse stage. In the late decomposition phase the litter might be composed of retarded part of the original litter and the part processed by microorganisms or animals (ex. dead body of fungi or animal feaces). In this phase, the litter in the bags was processed slowly. The retarded part of litter is difficult to utilize for the microorganisms or animals, and the part already processed might be recycled by the decomposers.

4. The litter bag fauna was dominated by Cryptostigmata (33.7% of total population) and Collembola (31.6%). The Cryptostigmata community was characterized by more species with relatively similar abundances, while the Collembola community was dominated by a few species. Cryptostigmata showed changes in the community throughout the period. Niche analysis suggested that the average niche size in terms of colonization time was similar between Collembola and Cryptostigmata, but the species packing was higher in the main species of Cryptostigmata which occupied similar niche positions on the gradient of colonization time.

5. The successional changes of the four collembolan species were explained by their feeding habits and were related to food availability at each decomposition phase. In contrast, successional changes of Cryptostigmata species were not simply explained by the feeding attributes of species. The wide utilization of resource gradients, together with the varied feeding habits of Cryptostigmata, might enable the coexistence of more species in their community than is the case with Collembola.

The activity of decomposers are important for nutrient cycling and maintenance of ecosystem productivity. Decomposition processes of pine needle litter occur as a result of interactions between microbial and soil animal populations. The roles of soil animals were important as a catalyzer of decomposition processes. The soil microarthropods contributed to the immobilization process of nitrogen and phosphorus through their grazing activities in the early decomposition phase (0-18 months) and the recycling of faeces and decomposition products in the late decomposition phase (21-48 months).

Key words: decomposition, pine needles, carbon and nutrient dynamics, fungal abundance, soil arthropods, Cryptostigmata, Collembola, feeding habit, gut contents, succession, community

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